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Confronting a morphological nightmare: revision of the Neotropical genus *Guatteria* (*Annonaceae*)

P.J.M. Maas[1], L.Y.T. Westra[1], S. Arias Guerrero[1], A.Q. Lobão[2], U. Scharf[3], N.A. Zamora[4], R.H.J. Erkens[1,5]

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Abstract A taxonomic revision of the genus *Guatteria*, including the former genera *Guatteriella*, *Guatteriopsis* and *Heteropetalum* is given. Within the genus *Guatteria* 177 species are recognized, 25 of which are new. Included are chapters on the history of the taxonomy of the genus, morphology, wood anatomy, karyology, palynology, chemistry, flower biology and pollination, dispersal, distribution and ecology, phylogeny and molecular studies, conservation, and uses. A synoptical key to all species is included, as well as two dichotomous keys, one for the species of Central America and Mexico, and one for the species of NE, E and SE Brazil. The species treatments include descriptions, full synonymy, geographical and ecological notes, vernacular names and taxonomic notes. For all species distribution maps are made. A complete identification list with all exsiccatae studied, an index to vernacular names and an index of scientific names is included at the end.

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INTRODUCTION

Guatteria is among the oldest still accepted genera of *Annonaceae* in the New World. *Annona* was published in 1753, followed by *Xylopia* in 1759, *Asimina* in 1763, and *Porcelia* and *Guatteria* in 1794 (Maas et al. 2011). In the 220 years of its existence over 425 species have been described in the genus with some years ago even 307 accepted names present (Erkens et al. 2008). At that time many new species were foreseen due to the large amounts of unidentified material in herbaria worldwide. Indeed, since then eight new species have been described (Lobão et al. 2010, Maas & Westra 2010, 2011, Arias G. et al. 2014, Lobão & Lopes 2014), and some 25 more are described in this publication. However, opposing the increase of species stands a decrease due to synonymization. For instance, a few years ago 40 names were synonymized into *Guatteria australis*, leading to a large reduction in species diversity in the genus (Lobão et al. 2011). More such reductions take place in this publication. For instance, 34 names are newly synonymized under *G. punctata* (bringing the total number of synonyms to 46) including the type species of the genus, *G. glauca* (for a further discussion about conservation and lectotypification of *Guatteria* see Van Setten & Maas 1990). The circumscription of *G. punctata* has always been problematic, but other species previously considered to be clearly circumscribed also disappear, such as for instance *G. recurvisepala* and *G. boliviana* that are now brought into synonymy with *G. ucayalina* (plus six more new synonyms).

This pattern is perhaps reminiscent of earlier days in the taxonomic history of *Guatteria* (more elaborately described by Erkens et al. 2008). After the description of the genus by Ruiz & Pavón (1794) the number of species steadily increased via for instance the works of Dunal (1817), De Saint-Hilaire (1824–1825), Von Schlechtendahl (1834), Von Martius (1841), Triana & Planchon (1862), Diels (1905, 1906, 1924a, b, 1927, 1931) and Fries (1938). At that point in time 'Sweden's grand old man of botany' (Buchwald 1970), Robert Fries, had taken a keen interest in the 151 species of *Guatteria* described and he worked on the only revision before the current one. He synonymized and transferred species but also described 106 new ones, and organized these species into 30 sections (Fries 1939). Later he erected two subgenera (Fries 1955a) and he reduced the number of sections to 22 (Fries 1959b). After his revision, Fries continued to be the main describer of new species in the genus (for details again see Erkens et al. 2008).

THE PIONEER OF ANNONACEAE SYSTEMATICS

Klas Robert Elias Fries (11 July 1876–29 January 1966; Fig. 1) was the author of the only comprehensive revision of *Guatteria* to date. Next to this revision he has left an extensive and impressive botanical record of accomplishment. In his work he covered three continents (Europe, South America and Africa) with works on taxonomy, phytogeography and mycology. He

[1] Naturalis Biodiversity Center, section Botany, P.O. Box 9517, 2300 RA Leiden, The Netherlands.
[2] Laboratório de Sistemática e Biogeografia, Setor Botânica, Departamento de Biologia Geral, Universidade Federal Fluminense, Rio de Janeiro, Brazil.
[3] Herbarium, Institut für Botanik, Universität Leipzig, Johannisallee 21–23, D-04103 Leipzig, Germany.
[4] Instituto Nacional de Biodiversidad (INBIO), Apartado Aereo 22-3100, Santo Domingo de Heredia, Costa Rica.
[5] Maastricht Science Programme, Maastricht University, Maastricht, The Netherlands.

Fig. 1 Potrait of Robert E. Fries at c. 28 years of age (original in the Regnellian Herbarium, Stockholm, Sweden).

has written many publications on his trips to Africa and wrote ground-breaking treatments on the east African mountain vegetation (Jonsell et al. 1991). Next to this extensive work he contributed greatly to the flora of Central America, South America and the West Indies, especially to the knowledge of the family of *Annonaceae*. He monographed the family in his 1959 contribution to Engler & Prantl's 'Die Natürlichen Pflanzenfamilien' (Fries 1959b). He was also strongly interested in mycology and made important contributions to that field, such as his collections from Bolivia (a region ill collected at that time). Today we can conclude that his most important scientific contributions have dealt mainly with *Annonaceae* and various groups of fungi (Unknown 1966).

In terms of his professional career Robert Fries was part of a botanical tradition. His father, Thore Magnus Fries (1832–1913), was professor of Botany at Uppsala University and his grandfather, Elias Magnus Fries (1794–1878), had been Scandinavia's most famous mycologist (Buchwald 1970). His career started at the age of 25 when he was part of an expedition to the northern part of Argentina and the South of Bolivia (Chardon 1947) which provided the basis for his doctor's degree at Uppsala University in 1905 (Unknown 1966). After this, he obtained a teaching position at Uppsala University and in 1915 he was appointed Professor Bergianus (director of the Hortus Bergianus) and director of the Bergius foundation at Stockholm, a position he retained until his retirement in 1944 (Chardon 1947, Unknown 1966). He also held many board positions. From 1928–1939, he was vice-secretary of the Academy of Sciences of Sweden; in 1939–1940, he became president of the latter Society and in 1942 he was vice-president. From 1934–1939 he was also president of the Botanical Society of Stockholm and member of the Dendrological Society (1927–1946), the Linnean Society of Sweden (from 1924–1947; honorary president from 1947 until his death) and the Botanical Society of Sweden (from 1943–unknown; Chardon 1947).

THE GUATTERIA PROJECT

Around 2000 a project was started at the Nationaal Herbarium Nederland - Utrecht Branch (now part of Naturalis Biodiversity Center, Leiden; Erkens & Baas 2008) to investigate *Guatteria* as part of the *Annonaceae* Research Project (Maas 1984). The project had the following main aims: 1) to revise the species of *Guatteria* based on a geographic division among coworkers; 2) to clarify the phylogenetic position of *Guatteria* within *Annonaceae*; 3) to elucidate the relationships between the genera in the *Guatteria* group; 4) to produce a phylogenetic tree containing a significant number of species of *Guatteria*; 5) to investigate the biogeographic history of the genus; and 6) to provide insight into the evolution of key morphological and anatomical characters.

REVISIONARY WORK

The revision of species diversity in *Guatteria* based on a geographical division proved fruitful. The southeastern Brazilian species were mainly investigated by Lobão for her thesis and in publications (Lobão & Mello-Silva 2007, Lobão et al. 2010, 2011, 2012, Lobão & Lopes 2014). Scharf et al. focused on species from the Guiana shield area (2005, 2006a, b, 2008) and made a contribution to the Flora of the Guianas (in prep.). Erkens et al. focused more on Central America, the Caribbean and non-Amazonian Colombia, as can be seen from the preliminary treatment for Flora Mesoamericana in Erkens' thesis (Erkens 2007) and several newly described species from that area (Erkens et al. 2006, Arias Guerrero et al. 2014, see also this publication). Susana Arias G. revised the West Colombian Andean species for her Masters thesis (Arias Guerrero 2011, unpubl. data). Also Zamora et al. have been working on especially the Costa Rican diversity (Zamora & Maas 2000, Erkens et al. 2006, see also this publication). Lastly, Maas et al. focused on Amazonian South America (Maas et al. 1988, Erkens et al. 2008, Maas & Westra 2010, 2011) but Maas also made contributions to many of the other publications mentioned above. For a more elaborate overview of publications on *Guatteria* see Erkens et al. (2012b).

This revision is the culmination of all this work. It will serve as a new taxonomic base line for future work, finally replacing Fries' 1939 revision. As such this revision fits in a long tradition of systematic work on *Annonaceae* (Chatrou et al. 2012a). The current revision recognizes 177 species of *Guatteria*. This means that *Guatteria* is no longer the largest genus within *Annonaceae* contrary to as stated before (Erkens et al. 2008) and cannot be seen as one of the largest genera of woody Neotropical trees any more.

THE PHYLOGENETIC POSITION OF GUATTERIA WITHIN ANNONACEAE

In morphological analyses of *Annonaceae* the position of *Guatteria* was unclear (e.g., Doyle & Le Thomas 1996) because many of the character states for *Guatteria* are homoplastic or unique within the family. Also the early molecular phylogenetic analyses placed *Guatteria* ambiguously with respect to its sister clades (Bygrave 2000, Richardson et al. 2004, Couvreur et al.

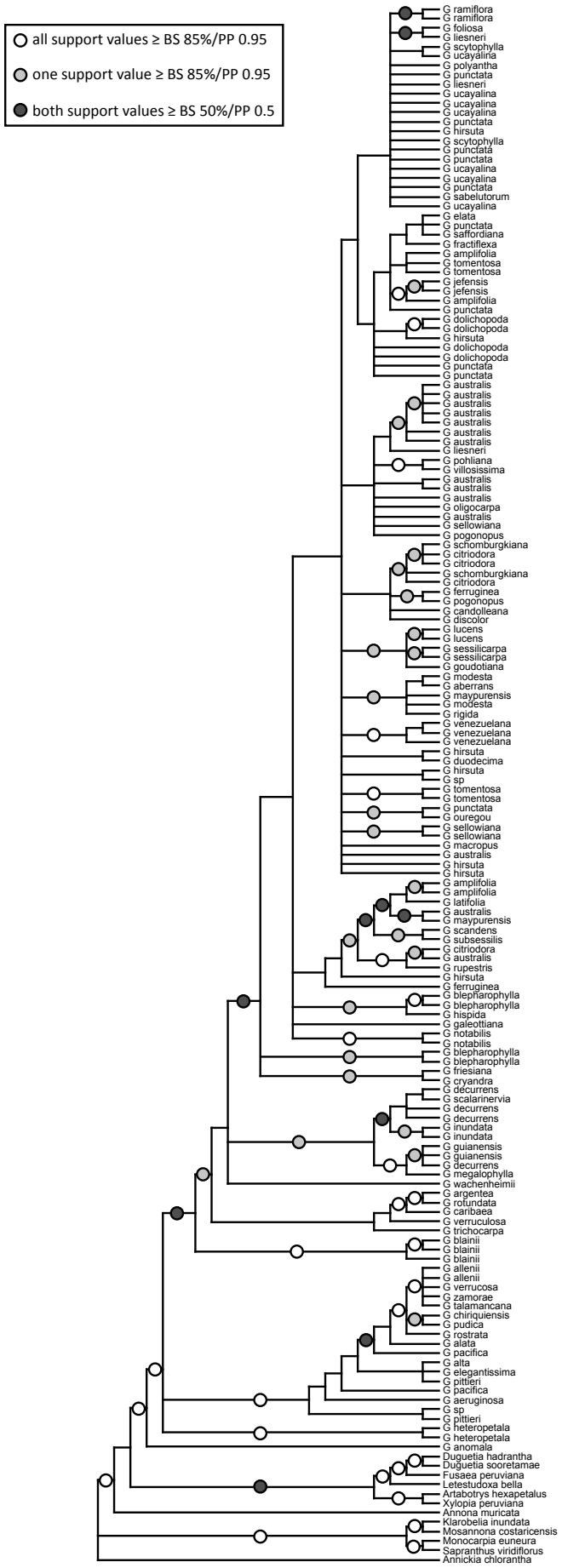


Fig. 2 Most parsimonious tree as published in Erkens et al. 2007 based on plastid *matK*, *trnLF*, *rbcL* and *psbA-trnH* sequences but updated for the taxonomy presented in this paper. Support value catagories are summaries of bootstrap percentages (BS) and Bayesian posterior probabilities (PP; for more details on the analyses see the original paper).

2008). It was clear, however, that the clade to which *Guatteria* belongs contains genera with African, Asian and South American origins (Doyle et al. 2004, Richardson et al. 2004, Couvreur et al. 2008), now called subfamily *Annonoideae*. A reconstruction specifically of the phylogenetic relationships within *Annonoideae* was undertaken in order to address the issue of the phylogenetic position of *Guatteria* (Erkens et al. 2009). Unfortunately, in that study there was still ambiguity with respect to the placement of four lineages (all classified as tribes by Chatrou et al. 2012b): *Guatterieae*, *Duguetieae*, *Xylopieae*, and the remainder of the species of this clade (*Annoneae*, *Monodoreae* and *Uvarieae*). The position of *Guatteria* at the end of a long branch might be cause for these alternative placements (due to long-branch attraction; Erkens et al. 2009). Subsequent, family-wide analyses have not been able to resolve this issue either (Couvreur et al. 2011, Chatrou et al. 2012b).

The phylogenetically (long branch) and morphologically (unique character states) isolated position of *Guatteria* might be explained by its biogeographical history. It was shown that the most likely distribution of the stem lineage of *Guatteria* was the African-North American region and a scenario of migration from Africa via Europe into Central and South America has been hypothesised for this genus (for an elaborate discussion on this and other scenarios see Erkens et al. 2009). Stepwise cooling from the Middle Eocene onwards removed frost-intolerant taxa from much of North America. In this scenario in the Middle/Early Miocene (between 18 and 11 Ma) the ancestors of *Guatteria* reached Central America, just before the northern climate became too hostile. In this situation any intermediate North American and European taxa went extinct and a phylogenetically isolated genus remains sitting on a long branch. Also, all taxa with intermediate morphological character states were removed and therefore it is now impossible to connect extant *Guatteria* to other *Annonaceae* genera morphologically (Erkens et al. 2009).

THE FORMER GUATTERIA GROUP

Until a few years ago four genera were thought, on morphological grounds, to be part of the so-called *Guatteria* group (Fries 1939, 1943, 1959b): *Guatteria*, *Guatteriopsis* R.E.Fr., *Guatteriella* R.E.Fr. and *Heteropetalum* Benth. The close affinity between these genera was established by many authors independently on morphological grounds (for details see Erkens et al. 2007a, Erkens & Maas 2008) and via more formal (molecular or morphological) phylogenetic analyses (He et al. 1999, Bygrave 2000). However, none of the latter studies had sufficient taxon sampling or enough data to adequately address the putative monophyly of these four genera. This question was specifically addressed in a molecular phylogenetic study and it was shown that *Guatteriopsis*, *Guatteriella* and *Heteropetalum* were actually nested within *Guatteria* (Erkens et al. 2007a). As a result the nested genera were transferred into *Guatteria* (Erkens & Maas 2008).

PHYLOGENETIC TREE OF GUATTERIA

A phylogenetic tree based on four regions of the plastid genome and containing c. 40 % of the species of *Guatteria* was constructed (Erkens et al. 2007a, b), but internal resolution in this tree proved to be weak (Fig. 2). Therefore, a completely new subgeneric classification of *Guatteria* is still premature because of the lack of molecular and morphological synapomorphies to define new sections (Erkens et al. 2007a, 2008). Currently, an improved version of this phylogenetic tree is being generated based on full plastome sequences (Erkens & Brandão, in prep.).

INFRAGENERIC BIOGEOGRAPHY OF GUATTERIA

The interesting question is what caused the lack of resolution in the phylogenetic tree of *Guatteria*. Three major biogeographical events in the history of the genus were reconstructed and hypothesised to be responsible for the pattern found (Erkens et al. 2007b). The oldest extant lineages of *Guatteria* can be found in Central America (Erkens et al. 2007b), except for the lineage leading to *G. heteropetala* (Erkens et al. 2007a). The Central American lineage has diversified and given rise to mainly endemic Central American species, which are morphologically clearly distinguishable. It is thought that a second trans-oceanic Miocene migration from Central into South America has taken place (in addition to the one leading to *G. heteropetala*) before the closing of the Isthmus of Panama, followed by a major diversification of the lineage within South America (mainly in the Amazon). Such a rapid and recent burst of diversification from the most recent common ancestor of the extant species can result in poorly resolved phylogenies (Richardson et al. 2001). The third important biogeographical event was the re-migration of several South American lineages into Central America via the closed Panamanian land bridge. These species are morphologically difficult to distinguish from each other, as is to be expected of young species. It can, therefore, be concluded that *Guatteria* is not an Amazonian centred genus sensu Gentry (Gentry 1982) but a genus with ample Miocene speciation following its dispersal into South America.

Although this rapid diversification of the 'South American Clade' within *Guatteria* (Erkens et al. 2007b) has led to a large amount of species, *Guatteria* itself does not constitute a radiation (Erkens et al. 2012a). *Guatteria* is in itself one of the larger annonaceous genera, but not larger than can be explained on the basis of stochasticity (actually, in comparison to its putative sister groups it is rather small). As a matter of fact, none of the largest genera in the family are the result of radiations (except perhaps *Goniothalamus*). The larger clades within *Annonaceae* probably did not result from intrinsic key innovations since lineage-through-time plots are fairly linear. This is generally associated with a constant rate of diversification. *Annonaceae* as a whole diversified at an overall steady rate (possibly due to low extinction rates; Couvreur et al. 2011).

INSIGHT INTO THE EVOLUTION OF KEY MORPHOLOGICAL AND ANATOMICAL CHARACTERS

The recent divergence of [some species of] *Guatteria*, the lack of phylogenetic structure and the absence of (key-)characters associated with speciation severely hampers character mapping onto a phylogenetic tree (Erkens 2007). Some characters have been tried (e.g., wood anatomical characters; Erkens et al. 2007a) but the evolution of most characters is still poorly understood. For instance, the indument (covering the whole plant in a species as *G. tomentosa*) is very easily recognizable and unidentified specimens can therefore often be assigned to species based on this. However, it is unclear whether or not indument types show homoplasy. This situation is comparable to the problematic use of the impressed secondary venation as a delimiting character for the *Guatteria amplifolia*-complex in Central America (Erkens 2007). There is one noteworthy exception (Maas & Westra 2011): species that are characterized by leaves with tiny warts (verruculae) on both surfaces (in combination with elongate and short-stipitate monocarps) belong to one particular clade that aligns with Fries' sect. *Mecocarpus*. However, the function of these warts is still unclear and their synapomorphic status is a matter of debate (Erkens et al. 2007a, Maas & Westra 2011).

GENERAL MORPHOLOGY

Habit

Species of *Guatteria* are trees, mostly medium-sized, or less often shrubs. The only lianescent species are the commonly collected *G. scandens* and the rarely collected *G. fractiflexa*, which can also be a facultative shrub. Incidental field notes also mention a liana habit in *G. beckii*, *G. flexilis* and *G. synsepala*. The height of the trees or shrubs generally varies from 1 to 40 m; among the exceptions are *G. grandiflora* up to 60 m tall and *G. modesta* up to 55 m tall. Small tree species or shrubs generally not exceeding 4 m in height are *G. delicatula*, *G. maypurensis* (both inhabiting savannas), *G. rupestris* and *G. stenophylla*. Some species can be very variable, e.g., *G. arenicola* with individuals in campinarana vegetation no more than 2–3 m high, but reaching up to 30 m in forests. Most species of *Guatteria* are quite slender with stems < 25 cm diam, but there are quite a few exceptions here, too, e.g., *G. cuatrecasasii* (up to 85 cm diam), *G. procera* (up to 90 cm diam), *G. modesta* (up to 1 m diam), and the huge Mexican/Central American species *G. grandiflora* which can have stems of up to 170 cm diam.

Leaves

The leaves are simple, entire, petiolate and estipulate. Leaf disposition, as in the vast majority of *Annonaceae*, is in 2 rows (distichous), particularly obvious in lateral branches. Petioles mostly are comparatively short, normally varying from 1–10 mm in length and 0.5–5 mm diam. The longest petioles were found in *G. chrysophylla* (15–30 by 4–6 mm), *G. paludosa*

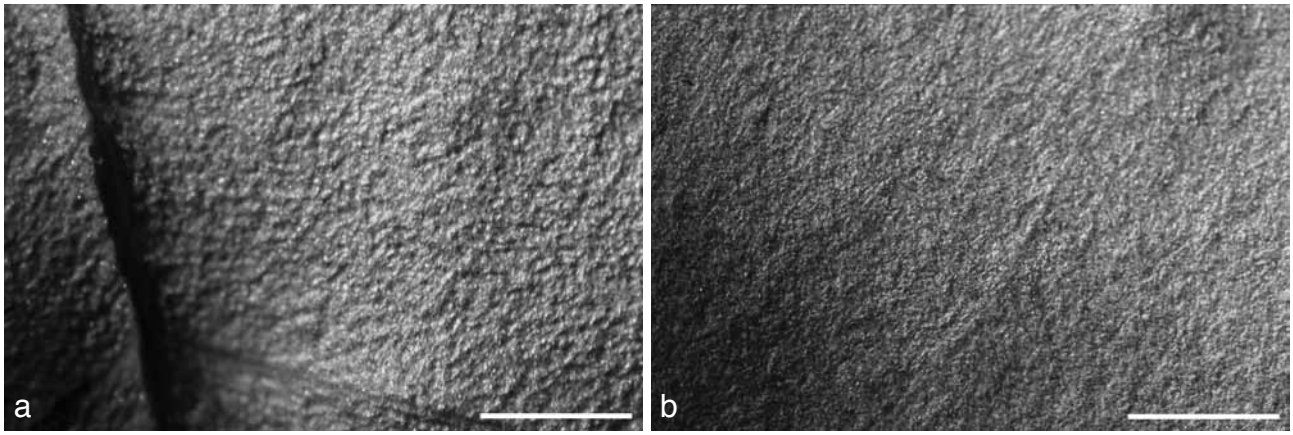


Fig. 3 Rugulose upper leaf surface, enlarged. a. *Guatteria anteridifera* Scharf & Maas; b. *Guatteria paludosa* R.E.Fr. (a: *Sabatier & Prévost 4936*, U; b: *H.D. Clarke 11004*, U). — Scale bar = 1 mm.

(15–30 by 3–4 mm), *G. castilloi* (20–35 by 1–2 mm) and *G. megalophylla* (15–50 by 3–10 mm). The shape of the lamina varies from elliptic, ovate, obovate, or narrowly so, or narrowly oblong-elliptic, obovate-oblong, etc. The texture varies from chartaceous to coriaceous, the surface varying from dull to shiny above, and is smooth in the majority, but verruculose both above and below in about 1/4 of the species; in few of the species, e.g., *G. anteridifera*, *G. ayangannae* and *G. paludosa*, the epidermal surface shows minute more or less circular sculptures when viewed with a powerful lens, indicated by the term scabridulous (Fig. 3). The lamina most often is between 10–30 cm long, with a length to width index varying from 1.5–≥ 7, but mostly between 2 and 5; the largest leaves up to 75 by 30 cm in size were found in *G. megalophylla*, while in about 10 species the lamina, as far as seen, does not exceed 10 cm in length, with *G. odorata* at the smallest extreme with leaves 5–6 by 1.5–2.5 cm in size. The apex of the lamina generally is acute or mostly acuminate, the acumen between 5–20 mm long (with few extremes to ≥ 30 mm long). A fairly small number of species has obtuse or even rounded apices, e.g., *G. castilloi*, *G. griseifolia*, *G. meliodora*, or emarginate in e.g. *G. blainii* and *G. emarginata*. The most extreme are probably the leaves of *G. clusiifolia* with a truncate apex. The base of the lamina varies from acute, attenuate, obtuse to cordate. The most common leaf base is acute, attenuate or obtuse. In the attenuate leaf base the extreme base is sometimes slightly decurrent as a wing along the petiole. A cordate leaf base is encountered in less than 10 species (e.g., *G. candolleana*, *G. friesiana* and *G. pudica*). Stem-clasping leaves are extremely rare and seen in only three species (*G. campinensis*, *G. longicuspis* and *G. tomentosa*), but note that in these three species the base can vary from stem-clasping to not stem-clasping. More generally, variation in shape of the leaf base within the same species is not uncommon, e.g., in *G. amplifolia* the base varies from obtuse, acute to cordate and in *G. hirsuta* from acute, obtuse to rarely attenuate or cordate. In c. 20 species the basal margins are revolute, one species (*G. revoluta*) is even named after that feature. The primary vein is impressed above in almost 50 % of the species. In a little over 10 % of the species the primary vein is flat to impressed, while in less than 10 % the primary vein is flat. A flat to raised primary vein is found in a little less than 10 % of the species. Species with a primary vein raised all along are quite exceptional (*G. alticola*, *G. beniensis*, *G. crassivenia*, *G. gentryi* and *G. pachycarpa*). The venation is brochidodromous, i.e. secondary veins joined together in a series of arches (loop-forming), mostly in the upper 1/3 to 2/3, and mostly eucamptodromous in the basal part, with secondary veins gradually diminishing inside the margin and connected to superadjacent ones by a series of cross veins without forming loops (Metcalfe & Chalk 1979: 30). In brochidodromous venation patterns the loops can be relatively thick and become lined-up in a (more or less undulating) marginal vein in a number of species (e.g., *G. guianensis*, *G. venosa*). The distance between loops and margin in most species varies between 1–5 mm, to 7 mm in few species. A notable exception is *G. sessilicarpa* with smallest distance between loops and margin 5–10 mm. The number of secondary veins varies widely within the genus, ranging from only 5 to as many as 35 on each side of the primary vein, but most species having between 10–20 pairs. Species with the lowest number are *G. acrantha* and *G. partangensis*, both with 6–9 pairs of secondary veins, and *G. elegans* with 5–8 pairs. The highest numbers occur in *G. guianensis*, *G. insculpta* (both with 20–35 pairs), *G. megalophylla* (15–35 pairs) and *G. venosa* (25–35 pairs). The secondary veins are distinct in close to 85 % of the species, and indistinct (hardly visible, sometimes difficult to count) in the remainder. In roughly 2/3 of the species the secondary veins are raised on the upper (= adaxial) side, while in the remainder the secondary veins are flat to/or impressed above, in few species strongly impressed (e.g., *G. megalophylla*, *G. punctata* p.p., *G. venosa*).

The angle of secondary veins with the primary vein ranges between 60° and 90°, exceptions are *G. elegans* (30–40°) and *G. campestris* (40–55°).

The tertiary venation is conspicuous in almost all species. It is hardly visible or even seemingly absent in a handful of species, namely *G. conspicua*, *G. decurrens*, *G. emarginata*, *G. friesiana* and *G. meliodora*. The tertiary veins are raised on the upper side of the lamina in 3/4 of the species, in the remaining 1/4 they are flat to impressed. Tertiary venation is mostly reticulate, but in less than 1/5 of the species it is percurrent (Metcalfe & Chalk 1979). A good example of percurrent tertiary venation is *G. ucayalina*.

Indument. Most species of *Guatteria* possess hairs on their leaves, young branchlets and flowering parts (particularly sepals and petals), whereas completely glabrous species are rare. The indument is composed of simple hairs only. In a few species, however, the hairs tend to be organized in tufts, almost suggesting stellate hairs (e.g., *G. stipitata*). For specific recognition it is important to know if the hairs are appressed or erect. This feature generally is quite reliable, although there are, unfortunately, some species where both erect and appressed hairs occur.

Inflorescences

Annonaceae show a variety of inflorescences. Fries (1919) was the first to publish a large article on the subject. In this paper he investigated 25 genera (as recognized at that time), mostly from material in spirit from the botanical museum in Uppsala (UPS) and the Botaniska Muséet in Stockholm (S). Later important papers on inflorescence structure are by Fries (1959b: 13–20) and Weberling & Hoppe (1996). Flowers in most species of *Guatteria* appear in the axils of leaves, and/or in the axils of fallen leaves. In little less than half of the species the flowers are solitary in the axils while between 35 and 40 % have 1–2 flowers in the axils, and in a minority (about 15 %) leaves can also harbour more than 2 flowers. The pedicels vary greatly within the genus, ranging from less than 5 mm to over 10 cm in length – but see also note in the last paragraph of this section! In most species the pedicels are between 10–40 mm long, while in about 10 % of the species the pedicel length is 10 mm or less (e.g., *G. blepharophylla* p.p., *G. campinensis*, *G. friesiana*, *G. schomburgkiana*). Pedicels over 40 mm long are found in roughly 15 % of the species (e.g., *G. alta*, *G. darienensis*, *G. dolichopoda*, *G. novogranatensis*, *G. pittieri*), with the longest exhibited by G. *grandipes* (to 90 mm) and *G. macropus* (to 120 mm). In a number of species the length increases to a greater or lesser extent between flowering and fruiting stage. There is also variation in diameter from c. 1 mm in many species to c. 2 mm in others, and increasing during fruiting stage to 5 mm (or even more). The pedicel, or flower stalk, is articulate mostly in the basal part. The articulation in *Guatteria* essentially is oblique, not transversal as in most *Annonaceae* (careful examination is often necessary!). The pedicel conforms to Fries's type 1 (Fries 1959b) in that it has a number of bracts in the part below the articulation with the two uppermost bracts placed immediately below the articulation, but no bracts above the articulation. There are usually between 5–8 bracts, and they represent leaves reduced to small scales. The lowermost bract is placed on the adaxial side, and in fact is the addorsed prophyll already noted by Fries (1911). The two uppermost bracts are usually the largest, placed at the lower and at the upper end of the oblique articulation, and they protect the developing flower bud in the very early stage (Fig. 4c). Bracts normally fall soon, and their presence can only be inferred from the number of scars that

Fig. 4 Inflorescence variation. a. *Guatteria terminalis* R.E.Fr.: Fruit terminating a lateral branchlet; b. idem, flower terminal on a small lateral branchlet; c. *Guatteria flabellata* Erkens & Maas: young axillary inflorescence with bracts before shedding, the two uppermost bracts enclosing the flower bud; d. *Guatteria modesta* Diels: axillary inflorescences on leafless branchlet formed in part by accessory buds; e. *Guatteria duodecima* Maas & Westra: axillary inflorescences, partly simple, partly with one lateral flower from axil of bract; f. *Guatteria ayangannae* Scharf & Maas: inflorescence with two foliaceous upper bracts; g. *Guatteria flagelliflora* Maas & Westra: much-branched inflorescence; h. *Guatteria scalarinervia* D.R.Simpson: inflorescence on small trunk or large branch clearly showing branching patterns; i. *Guatteria ferruginea* A.St.-Hil.: old inflorescence on trunk; j. *Guatteria notabilis* Mello-Silva & Pirani: terminal 2-flowered inflorescence with all (partly foliaceous) bracts in place; k. same, 3-flowered rhipidiate inflorescence (a, b: *Farfán et al. 995*, WAG; c: *Croat 19183*, WAG; d: *Mutis 4486*, US; e: *Chatrou et al. 25*, U; f: *H.D. Clarke et el. 9819*, U; g: *Vásquez et al. 22500*, WAG; h: *Gentry et al.77361*, U; i: *Amorim et al. 818*; j: *Irwin et al. 22671*, U; k: *Hatschbach 64801*, U).

remain for a shorter or longer time. Among the few exceptions is *G. ayangannae*, an endemic of Guyana, where the two upper bracts are foliaceous and mostly persist until flowering time (Fig. 4f). Incidentally a bract enveloped into a (small) leaf may be found at random in many species.

Inflorescences in *Annonaceae* are of the determinate type (also termed monotelic or anthotelic), i.e., with the axis always ending in a terminal flower (see also Briggs & Johnson 1979 and Weberling 1981, 1989). The flowers in *Guatteria* actually are terminal on very short branches (brachyblasts) from the axils of leaves. Only in few species do flowers terminate normal leafy branches, namely *G. acrantha*, *G. grandiflora*, *G. notabilis* and *G. terminalis* (Fig. 4a, b). *Guatteria blainii* must be mentioned here as well because, superficially, it seems to have both axillary and terminal flowers. Careful inspection, however, shows that most seemingly terminal flowers in this species are in fact still axillary due to abortion of the main shoot apex; nevertheless, true terminal flowers also occur, but remain rare. Following Fries, the transition is best understood – without pretending to be a phylogenetic sequence! – starting with *G. terminalis* (Fries 1919: 32 et seq., as '*G. glauca*'). Here the single flowers stand on the top of normal leafy twigs, but also on somewhat smaller lateral twigs originating from axils, with leaves of normal shape, but of smaller size (Fig. 4b). A markedly oblique articulation is found c. 1–2 cm below the flower and showing the attachments of the two bracts continuing the leaf disposition in two alternating rows. The lower of the two bracts often is still in place and is foliaceous, i.e., with the shape of a normal leaf, but of (more or less) smaller size. The upper bract already had dropped in all material that was available, and could not be studied. Looking at a branch of *G. terminalis* in its entirety it is not difficult to envisage the suppression of apical flower development and at the same time an extreme reduction of axillary twigs to minute short shoots, the leaves of which have become reduced to small scale-like bracts (Fig. 4c). *Guatteria acrantha*, a recently discovered and described endemic of southern Panama, is very similar to *G. terminalis*. Another recently described species, *G. notabilis*, is remarkable in a number of aspects as shown in an illustration by its authors (Mello-Silva & Pirani 1988). Here the terminal inflorescences bear 1–3 flowers (Fig. 4j, k). The first flower is formed at the end of a leafy twig in a comparable way as in *G. terminalis*, and is subtended by two foliaceous bracts with the lower one being the largest. The upper one usually drops early, whereas the lower one is often present with the flower. From the axil of the lower bract often a second flower develops. This flower is subtended by two bracts. These bracts have the characteristic shape for the genus: obovate and more or less narrowing towards the base, and the upper part with incurving sides to protect the developing flower bud. Both these bracts are shed early. Exceptionally 3-flowered inflorescences occur, the third flower originating from the axil of the lower bract of the second flower (Fig. 4k). The result is the rhipidiate arrangement common in many genera of *Annonaceae*, but not in *Guatteria*.

Perhaps the oddest member of the genus to be mentioned here is *G. grandiflora*, occurring not only with terminal solitary flowers, but also quite often with 2–few-flowered terminal panicle-like inflorescences. In addition to terminal flowers there are also flowers on small axillary twigs. The inflorescences seem to branch dichotomously, without showing the familiar pattern of axillary shoots from axils of leaves or bracts. On closer look partial fusion of axes (concaulescence) appears to account for what seemed strange at first. Fries (1939) gave analyses based on several herbarium specimens which he illustrated with drawings (1939: 293–296, f. 1; Fig. 41). The small axillary twigs of *G. grandiflora* just mentioned are comparable to inflorescences in other *Guatteria* species, distinct mainly by the elongate internodes between the bracts. Paired flowers in the axils can originate in two ways (Fries 1919). One is that a serial accessory bud situated below the first bud also develops a flower (Fig. 4d). There appear two flowers in a more or less parallel stage of development ('einander gleichwertig', Fries 1919) (Fig. 4e). The second possibility is development of a lateral shoot from the axil of a bract of the first-order stalk. The two flowers then are in successive stages of development ('Die zweite Blüte … die Tochterblüte der ersten und nicht gleichwertig mit dieser', Fries 1919). It is likely that additional flowers that appear, often after the leaf has fallen, can originate via both ways. However, because of the highly compact inflorescence structure of many *Guatteria* species it is often difficult to determine whether a flower arose from an accessory bud or from the axil of a bract extremely close to the base. A peculiar species is the recently described *G. flagelliflora* where inflorescence branching has taken place many times (Fig. 4g). In the cauliflorous *G. scalarinervia* the inflorescences are much more compact, but branching can still be seen (Fig. 4h). In other cauliflorous species, e.g., *G. ferruginea*, *G. scandens*, flowers appear as if implanted in the callous tissue that had been forming as inflorescences became older (Fig. 4i). More morphological study is needed here, perhaps best by observing living plants during growth stages. Also the role of accessory buds is important, particularly regarding the question of whether one or (many) more accessory buds might be involved.

A final note should be made regarding the use of the term pedicel. In our descriptions this refers to the flower stalk as we intuitively see it in the leaf axils and as sticking out from the compact inflorescences that can be observed on older leafless parts of the plant. Strictly speaking, only the part above the articulation should be termed pedicel, the part below the articulation being a short shoot as explained above. For practical descriptive reasons we refrained from discriminating between pedicel proper and the supporting short shoot in measuring the flower stalk over the whole length, except for e.g., *G. terminalis*, where pedicel length is measured from the articulation upward. In *G. grandiflora* the free parts of the flower stalks are measured as pedicels.

Flowers

Flower buds are generally depressed to broadly ovoid in outline, rarely conical (e.g., *G. friesiana*). Their apex is generally obtuse, but in a few species the apex is distinctly pointed (Fig. 5).The sepals are always much smaller than the petals. In most species the sepals are free, but in a few species they are basally connate. Their shape varies from ovate-triangular to broadly ovate-triangular. The sepals are appressed to the petals or partly or completely reflexed. The length of the sepals ranges from 2–20 mm; the length is mostly averaging from 2–10 mm. A handful of species has sepals larger than 10 mm. Extremes are *G. latifolia* from SE Brazil with sepals of 10–20 by 10 mm and *G. talamancana* from Central America with sepals of 15–20 by 10–15 mm. Petals are in two 3-merous whorls, much surpassing the sepals in size. The aestivation is imbricate, exceptionally valvate (e.g., *G. blepharophylla*, *G. heteropetala*), usually only visible in young buds. The petals generally soon spread while continuing to develop and become larger. While the growth phase takes a certain amount of time, anthesis itself, as is generally the case in *Annonaceae*, lasts only a short time. In the short anthesis phase the petals have their maximum size before they are shed. As mature flowers can be considerably larger than flowers in the development stage immediately preceding it, and given the fact that good ripe flowers may still not have been collected in many species, the measurements in the descriptions in a number of species may have to be read with caution. The colour most often reported, apart from green,

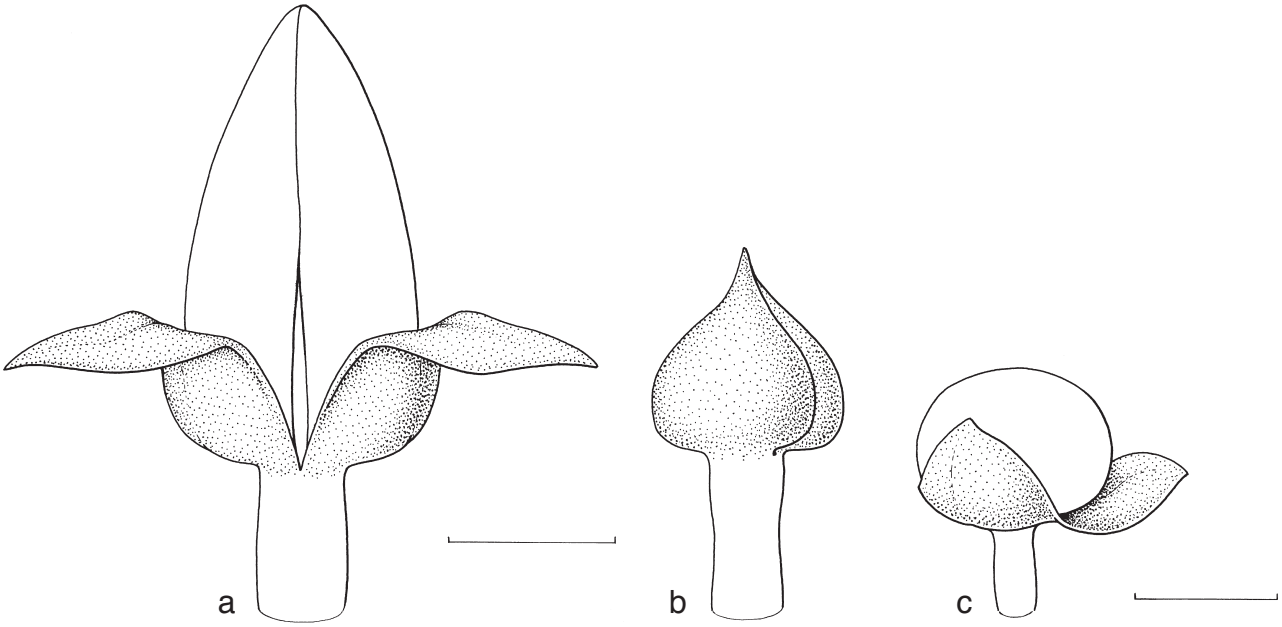


Fig. 5 Flower bud shapes. a. Conical; b. pointed; c. rounded. — Scale bars = 5 mm. — Drawing: Esmée Winkel 2014.

is (shades of) yellow or cream; white has been reported on various occasions as is also the case with pink or red (e.g., *G. stipitata*). The chocolate-brown petals of *G. aberrans* and the lead-coloured petals of *G. terminalis* deserve special mention. The petals of the two whorls generally are of comparable size and shape. The most notable exception is *G. heteropetala* where the outer petals are only about half the size of the inner petals. This feature formed the main reason for placing this species in a separate genus *Heteropetalum.* Also *G. vallensis* must be mentioned where the inner petals, as far as seen in the type collection, are about half as long as the outer petals (Fig. 70f). The general shape varies from elliptic, ovate-elliptic, ovate, obovate, to narrowly so, or oblong in various combinations. More rare are, among others, ovate-trullate, obtrullate or flabellate shapes (*G. flabellata*). In the descriptions usually one set of measurements is given for all six petals, except where outer and inner whorl differ visibly. Petal length in *Guatteria* varies from 5–50 mm, but generally is over 10 mm. Species with the smallest petals are *G. emarginata* (5–9 by 6–7 mm) and *G. minutiflora* (5–15 by 3–7 mm). The largest petals are found in e.g., *G. grandiflora* (15–40 by 5–13 mm), *G. ucayalina* (20–45 by 7–25 mm), *G. punctata* (10–50 by 5–20 mm), *G. flabellata* (25–50 by 10–40 mm). The torus varies from broadly ovoid to conical, shortly cylindrical or cushion-shaped with a convex, flat or concave depression at the top, rarely with a flat top (*G. heteropetala*) (see Van Heusden 1992). There are many stamens in the genus *Guatteria*. They are provided with a very short filament; the anthers are extrorsely dehiscent. All species have a distinct apical and discoid prolongation of the connective, the so-called connective shield (Fig. 6). The connective shield mostly is flat, but in a few species it is adorned with a swelling in the centre, called umbo. The presence of this umbo is not constant within a species. The connective shield is covered with minute papillae or less frequently with tiny simple, erect hairs, or it is glabrous. The length of the stamens mostly varies from 1–2 mm, exceptionally more. The largest stamens are found in *G. grandiflora*, *G. guianensis*, *G. paludosa* and *G. pittieri*, where the stamens can reach a length of 3 mm. Carpels are free, generally numerous, varying from 1.5–4 mm long, hairy, narrowed into a style or not, the stigma obovoid, discoid, or obconical, sometimes cup-shaped and grooved, ovule 1, basal (Van Heusden 1992).

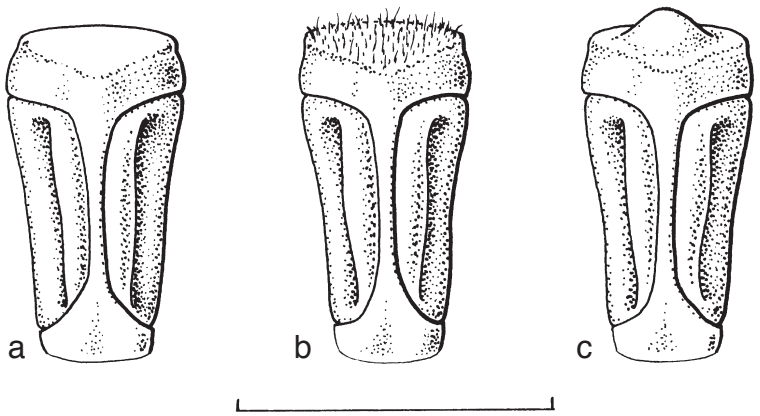


Fig. 6 Stamens, variation in connective shield. a. Papillate or glabrous; b. hairy; c. umbonate. — Scale bar = 1.5 mm. — Drawing: Esmée Winkel 2014.

Fruit

The fruit in *Guatteria* is apocarpous and composed of few to many, free fruitlets, or monocarps. The shape of the monocarps is generally ellipsoid, occasionally narrowly ellipsoid, and rarely globose. *Guatteria maypurensis* is the only species of *Guatteria* with narrowly oblongoid monocarps. In a few species the monocarps are narrowly ellipsoid and fusiform (e.g., *G. hispida* and *G. inundata*). In the latter the narrow monocarps are pointed at both ends, a unique feature within the genus. The length of a monocarp body varies from 5 to 35 mm, with the smallest monocarps of 5–7 mm long seen in *G. delicatula* and *G. monticola*, and the largest ones reaching a length of up to 30 or even 35 mm in *G. hispida*, *G. inundata*, *G. talamancana* and *G. trichocarpa*. The length of the fruiting pedicels varies from of a few millimeters up to 50 mm, and exceptionally to over 100 mm long (*G. macropus*). In a few species, however, the fruit may even be almost sessile (e.g., *G. schomburgkiana*). The monocarps are fleshy in texture. They generally mature to black or purple-black. Monocarps in herbarium specimens have a colour varying from black to brown. The number of monocarps per fruit generally varies from 10–75. In a few species, e.g., *G. ayangannae* and *G. anteridifera*, the number of monocarps is lower than 10, whereas in several species, e.g., *G. dolichopoda*, *G. griseifolia*, *G. hirsuta*, *G. meliodora*, *G. punctata*, *G. saffordiana* and *G. scytophylla*, up to 100 monocarps are encountered. Each monocarp is generally placed on top of a fleshy stalk, often red-coloured in vivo, termed the stipe. The stipes generally have a length between 5–25 mm. In *G. australis*, *G. latifolia*,

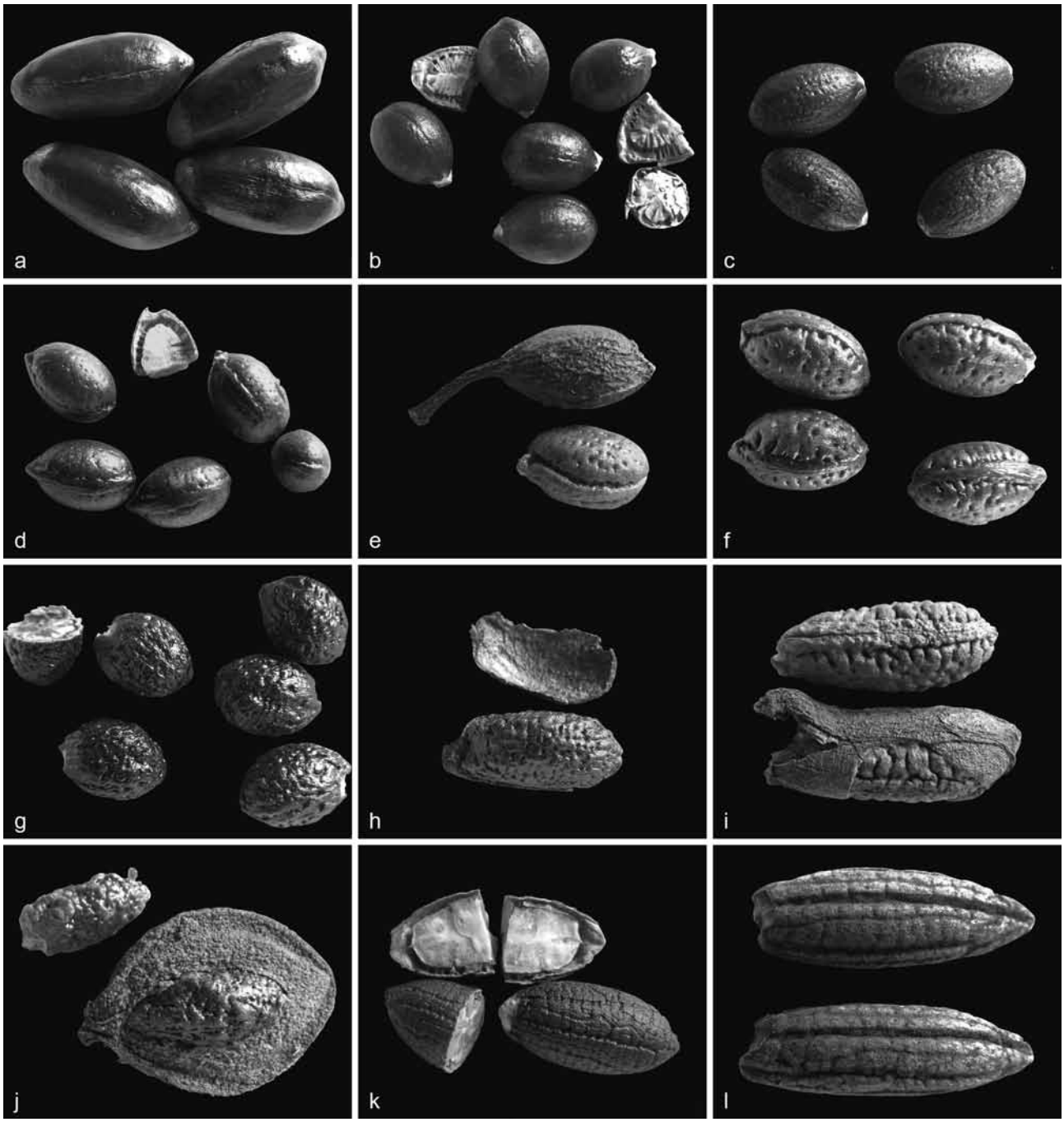


Fig. 7 Variation in seed sculpture. a. *Guatteria discolor* R.E.Fr.: smooth, raphe not distinct; b. *G. ucayalina* Huber: smooth to pitted, raphe flat; c. *G. amplifolia* Triana & Planch., d. *G. ferruginea* A.St.-Hil., e. *G. beckii* Maas & Westra, and f. *G. amplifolia* Triana & Planch.: pitted, raphe raised; g. *G. australis* A.St.-Hil. and h. *G. pakaraimae* Scharf & Maas: rugulose, raphe not distinct; i. *G. griseifolia* Maas & Westra: rugose, raphe raised; j. *G. verrucosa* R.E.Fr.: rugose, raphe not distinct; also note thick fruit wall; k. *G.decurens* R.E.Fr. and l. *G. blepharophylla* Mart.: longitudinally and transversely grooved, raphe not distinct (a: *Grenand 554*; b: *A.L. Gentry 6745*; c: *Liesner et al. 15199*; d: *Mori & Benton 12993*; e: *Arroyo et al. 2638*; f: *Mori & Kallunki 3046*; g: *G. Hatschbach 40693*; h: *H.D. Clarke et al. 10861*; i: *Neill et al. 12948*; j: *Haber 3893*; k: *Croat 20759*; l: *Amaral et al. 674*, all U).

G. ouregou, *G. punctata* and *G. scytophylla*, however, the stipes can grow out to a length of c. 30 mm, while in *G. ucayalina* stipes of even up to 50 mm are found. On the other hand, in a few species, the stipes are strongly reduced in length or virtually lacking. Examples of species with strongly reduced stipes between 0–2 mm are: *G. arenicola*, *G. blainii*, *G. heteropetala*, *G. pachycarpa*, *G. ruboides*, *G. schomburgkiana* and *G. sessilicarpa*. The monocarps are placed on a fruiting receptacle of 3–14 mm diam (Van Setten & Koek-Noorman 1992). The mature fruits in the great majority of species of *Guatteria* lack an indument or are covered with an indument of appressed (or rarely erect) hairs when young to become glabrous soon. In a few species the monocarps are covered with long-persisting hairs. Examples are *G. hispida* where the indument consists of erect, stiff hairs and *G. grandipes* with a rather dense indument of erect hairs. The wall of the monocarps is generally between 0.1 and 0.5 mm thick in dried state ('in sicco'), in a few species it can reach 2–3 mm (in *G. chrysophylla*, *G. clusiifolia*, *G. sessilicarpa* and *G. trichocarpa*), or even 5–6 mm (*G. pachycarpa* and *G. verrucosa* (Fig. 54b, 7j)). One should realize that in vivo the wall of the monocarps is fleshy, but that it shrivels considerably during the drying process. In a species like *G. pastazae*, for example, the wall is 0.5–1 mm thick in sicco, but measured from material preserved in spirit its wall is up to c. 4 mm thick.

Each monocarp has 1 seed, which is always basally attached. The seeds are generally ellipsoid in outline, whereas narrowly ellipsoid, narrowly ovoid or globose seeds are rarely met with. The apex of the seeds is obtuse, except in some species where it is distinctly pointed (e.g., *G. confusa*, *G. notabilis* and *G. friesiana*). The seed length varies from 5 to 25 mm. Seeds vary from light to dark brown in colour and are often more or less shiny. The surface of the seeds is quite variable from smooth to highly sculptured, see the discussion below. The raphe is usually quite distinct, but in some species is an indistinct structure. It can be either an impressed rib, a flat rib, or a distinctly raised rib. A rudimentary aril according to Van Setten & Koek-Noorman (1992) is often present. It is a structure of 0.1–3 mm high, consisting of sometimes longitudinally elongated, swollen and/or collapsed cells, forming a rib around the hilum. The hilum is mostly transversely elliptic, 1.5–6 mm wide, sometimes V-shaped (Van Setten & Koek-Noorman 1992). In some species, like *G. heteropetala*, the seed wall has a small air gap along the raphe. This air gap is probably an adaptation to dispersal by water. Ruminations in the seeds of *Guatteria* are spiniform or lamellate (often in 4 parts). A micropylar plug is absent or very small.

For descriptive purposes the primary focus is on the seed surface. Anatomical features, e.g., aril, hilum or ruminations, are not mentioned or only incidentally so. The reader is referred to the extensive survey of annonaceous seeds by Van Setten & Koek-Noorman (1992).

Five categories can be distinguished as to seed surface (Fig. 7):

1. Smooth seeds. Rarely encountered (e.g., *G. discolor*). Most species with smooth seeds occur in the Amazon Region or in the Guianas and one species in Central America.
2. Pitted seeds. This is the most common seed type with almost 50 % of all species showing this feature. Pitted seeds occur all over the Neotropics, but it is noticeable that many species from SE and E Brazil in particular show this seed type.
3. Rugulose seeds in which the surface is slightly rough. This is not the most common seed type in the genus. It is encountered throughout the Neotropics.
4. Rugose seeds. A very rough, almost brain-like surface characterizes these seeds. This is the secondmost common seed type in the genus. Most of the species which fall into this category occur in Central America and the Pacific coast of Colombia. A few species occur in the Amazon Region.
5. Longitudinally and transversely grooved seeds. A quite common seed type. Most species belonging to this category belong to Fries's sect. *Mecocarpus* and are confined to the Amazon Region. *Guatteria caribaea*, however, the only species of the genus occurring in the Lesser Antilles, shows this seed type as well.

It should be emphasized that these seed types are not always sharply distinct, and intermediates may be found.

LEAF ANATOMY

(J. Koek-Noorman, Ds. Van Haaftenlaan 28, 3984 NR Odijk, The Netherlands)

A leafanatomical survey of genera of *Annonaceae* in the Neotropics was done by Van Setten & Koek-Noorman (1986). This involved all 38 genera as then known and a total of over 200 species. Detailed studies were carried out later by Van Marle on *Pseudoxandra* (2003) and on the three related genera *Bocageopsis*, *Onychopetalum* and *Unonopsis* (2007). No detailed study on *Guatteria* as a whole exists yet. The short description that follows here is based on the study by Van Setten & Koek-Noorman (1986).

Cuticle — adaxially 0–6 µm, abaxially 0–2 µm, with a smooth outer layer without alveolar material wax.

Epidermis — 1–2-layered; stomata present on the abaxial and less numerous on the adaxial epidermis, paracytic with the subsidiary cells parallel to the guard cells; striations are lacking. Unspecialized cells polygonal with weakly to strongly undulating anticlinal cell walls; druses numerous, both abaxially and adaxially, one per cell, to (occasionally) absent.

Primary vein — composed of a central xylem body with the phloem tissue found along the abaxial side and intruding in the xylem body, but lacking on the adaxial side.

Mesophyll — dorsiventral, palisade parenchyma 1–3(–4)-layered; or often isobilateral with one additional abaxial layer. Oil cells round to oval, often present in sponge parenchyma. Angular ideoblasts with amorphic silica contents, often present near the end of the smallest veins in the sponge parenchyma. Druses often found near the primary vein. Sclerenchymatic cells common, present in part of the species as branched to stellate astrosclereids, in the other species as poorly branched, thick-walled osteosclereids. Bundle sheath extensions of the smaller veins are rather short, not reaching up to the epidermis.

Discussion

All leafanatomical features found in *Guatteria* are found in other *Annonaceae* as well. Many features vary to a certain extent within genera, sometimes even within specimens. With this in mind, we can say that the genus *Guatteria* is characterized by a combination of the following characters: the structure of the primary vein, together with the frequent angular ideoblasts containing amorphous silica, the presence of stomata in the adaxial epidermis, and the occurrence of sclereids in the mesophyll. Apart from *Guatteria*, this combination is only found in the genera of the *Unonopsis* group (*Bocageopsis*, *Onychopetalum*, *Unonopsis*). These three genera however share the presence of oil cells in or immediately below the often papillate epidermis, features not found in *Guatteria*. The minute warts (verruculae) found in leaves of a number of *Guatteria* species after drying, notably in what was treated as sect. *Mecocarpus* (Maas & Westra 2011), very probably are caused by osteosclereids. See also in this context the study on *Pseudoxandra* (Van Marle 2003), showing an excellent photograph of an osteosclereid reaching from the upper down to the lower epidermis. It may safely be assumed that such osteosclereids manifest themselves as the

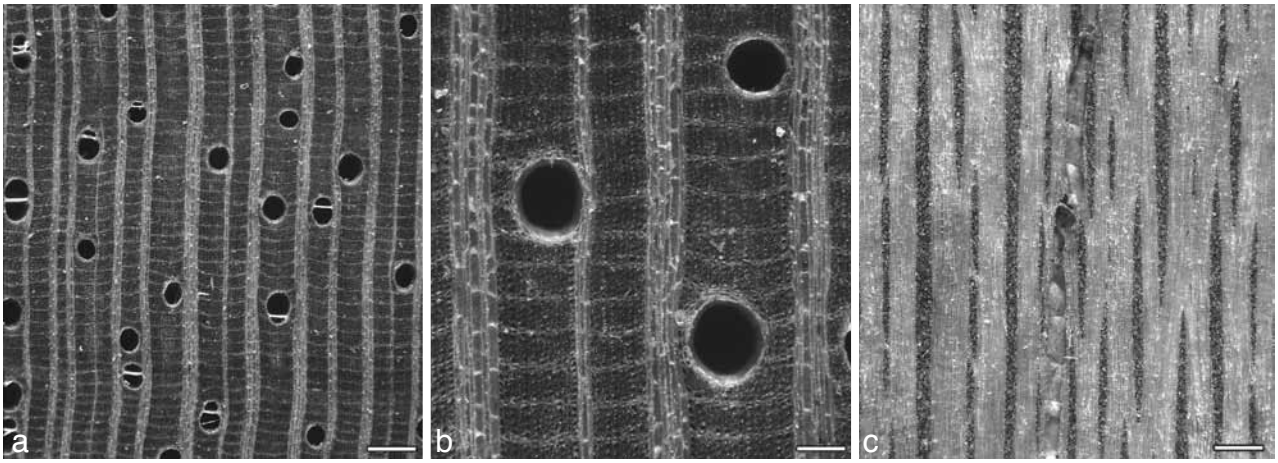


Fig. 8 Wood of *Guatteria discolor* R.E.Fr. a. Cross section; b. detail of cross section to show vessels with surrounding (vasicentric) parenchyma; c. tangential section, note high and many-celled rays (all: *Krukoff 7047*, Uw 8134). — Scale bars: a, c = 500 µm; b = 165 µm.

minute warts resulting from shrinkage of the mesophyll in dried leaves of this genus. It is likely that a similar process occurs in *Guatteria*, but this needs further investigation.

WOOD ANATOMY

Wood of *Annonaceae* generally is easy to recognize due to some characteristic features, e.g., broad and high multiseriate rays, and numerous tangential parenchyma bands forming a fine cobweb-like pattern when viewed with a good hand lens or even the naked eye (Fig. 8). A recent paper on wood of many annonaceous genera seen in the light of modern phylogenetic-taxonomic insight and with emphasis on hand lens observation has been published by Koek-Noorman & Westra (2012).

Papers on anatomy of wood of *Guatteria* on the microscopical level have been few so far. Hess (1946) gave a description on the genus level. Loureiro gave descriptions of *G. scytophylla* and *G. punctata* (as *G. olivacea*) (Loureiro 1970), and *G. citriodora* (as *G. paraensis* (Loureiro 1971)). (Note that *G. boyacana* (Kribs 1950, 1968) should now be referred to *Pseudomalmea*, see section on Excluded species.) The most extensive paper on *Guatteria* to date came from León H. (2006) who studied 12 species, reduced to 7 species in the current revision, viz. *G. discolor*, *G. hirsuta* (incl. *G. curvipetala*, *G. laurina*, *G. pilosula*), *G. megalophylla*, *G. modesta* (incl. *G. chlorantha*), *G. punctata* (incl. *G. olivacea* and *G. poeppigiana*), *G. saffordiana*, *G. schomburgkiana*, *G. stipitata* and *G. ucalayina* (incl. *G. cardoniana*).

Species of *Guatteria* often can be recognized by a relatively large number of broad rays and vessels often of fairly large diameter and mostly solitary. The most notable feature of *Guatteria* wood is the presence of a complete layer of parenchyma cells around the vessels, visible in cross sections as narrow vasicentric rings (Fig. 8a, b).

It may be safely concluded that the homogeneity in the wood structure of *Guatteria* as it fits in with that of the *Annonaceae* in general is confirmed in all research done so far. Among the very few exceptions are *G. heteropetala* with small vessels situated in a mass of very thin-walled, wide-lumen parenchyma cells, and with scant vasicentric parenchyma, and *G. grandiflora* with small vessels (< 80 µm diam) often in multiples or clusters of 2–5 cells, and without or with incomplete vasicentric parenchyma (Koek-Noorman & Westra 2012, as *G. anomala*). The mention of radial vessels in *G. modesta* (as *G. chlorantha*) by León H. (2006) deserves attention. It indicates the apparently rare occurrence of these structures.

In the one Neotropical lianous species we could examine, *G. scandens*, the vessel diameter gradually increases from the centre towards the periphery, and does not show the sharp transition from normal wood to liana wood as seen in (e.g.) the African genera *Friesodielsia* or *Toussaintia* (Koek-Noorman & Westra 2012).

KARYOLOGY

(R.D. Brandão, Maastricht Science Programme, Maastricht University, Maastricht, The Netherlands)

Relatively many species of *Guatteria* have been investigated in comparison to other *Annonaceae* genera with respect to their karyotype. This is mainly due to the work of Morawetz & Waha (1985) who studied most of the species in this review. Yet, from all 177 recognized species in this revision only 20 (12 %) have a known karyotype (Sauer & Ehrendorfer 1984, Morawetz & Waha 1985, Bennett & Leitch 2012). All material of *Guatteria* investigated so far have a tetraploid genotype with 2n = 28 (Table 1) and a base number of x = 7 (Fig. 9). The similarity found among *Guatteria* species contrasts with what was found in *Annona* (including *Rollinia*) and *Duguetia* (in tribes *Annoneae* and *Duguetieae*, respectively, together with *Guatterieae* in *Annonoideae*). Within *Annona* and *Duguetia*, diploid species seem to be the most frequent, followed by tetraploids. Less frequently, hexaploid species and even triploid (two out of seven analysed specimens of *Duguetia furfuracea*) were identified (Sauer & Ehrendorfer 1984, Morawetz 1986b, Maas et al. 2003, Foluronso & Olorode 2007, Bennett & Leitch 2012).

It is noteworthy that the base chromosome number x = 7 observed in all investigated *Guatteria* contrasts with the most frequently seen base number in *Annonaceae* (x = 8), observed in the basal *Annonaceae* genus *Anaxagorea*, as well as in *Artabotrys*, *Cananga*, *Cyathocalyx*, *Duguetia*, *Uvaria*, *Xylopia*, etc. However, the base number x = 7 was also found in *Ambavia*, *Annona*, *Cleistopholis*, *Mezzettia* and *Tetrameranthus*. Base number x = 9 has also been identified in other *Annonaceae* genera (e.g., *Cymbopetalum* and *Polyalthia* p.p.). Genera with base number x = 7 are believed to have developed independently from x = 8 and x = 9 (Morawetz 1986a, Doyle & Le Thomas 1996) by descending dysploidy (i.e., chromosome number reduction due to genome restructure with or without significant loss of genetic material). This hypothesis is supported by the differences in karyotypes and nuclei structures observed among the different genera (Morawetz & Waha 1985). However, due to new insights into the phylogenetic relationships

Table 1 *Guatteria* species for which karyoptype was investigated.

Taxon	Collector and number	2n =	Ploidy level	Reference
Guatteria amplifolia	*Ehrendorfer 6400-2001*	28	4	(Sauer & Ehrendorfer 1984)
G. australis	*Morawetz 11-101280*	28	4	(Morawetz & Waha 1985)
G. blepharophylla	*Morawetz & Coêlho 19-10883*	28	4	(Morawetz & Waha 1985)
G. brevicuspis[6]	*Morawetz et al. 11-6983*	28	4	(Morawetz & Waha 1985)
G. campinensis	*Morawetz & Coêlho 31-24883*	28	4	(Morawetz & Waha 1985)
G. friesiana	*Morawetz & Coêlho 12-10883*	28	4	(Morawetz & Waha 1985)
G. gomeziana[1]	*Morawetz 11-13381*	28	4	(Morawetz & Waha 1985)
G. hilariana[1]	*Gottsberger 11-2568*	± 28	4	(Sauer & Ehrendorfer 1984)
G. hispida	*Morawetz & Coêlho 12-25883*	28	4	(Morawetz & Waha 1985)
	Morawetz & Coêlho 21-25883			
G. aff. *inundata*	*Morawetz & Coêlho 11-18883*	28	4	(Morawetz & Waha 1985)
G. klotzschiana[1]	*Morawetz 11-281280*	28	4	(Morawetz & Waha 1985)
G. lanceolata[2]	*Morawetz & Coêlho 11-11883*	28	4	(Morawetz & Waha 1985)
G. maypurensis	*Morawetz & Coêlho 22-23883*	28	4	(Morawetz & Waha 1985)
G. megalophylla	*Morawetz & Coêlho 12-15883*	28	4	(Morawetz & Waha 1985)
	Morawetz & Coêlho 31-15883			
	Morawetz & Coêlho 12-23883			
G. multivenia[3]	*Morawetz & Coêlho 11-23883*	28	4	(Morawetz & Waha 1985)
G. obovata[4]	*Morawetz & Coêlho 16-18883*			
	Morawetz et al. 23-13983	28	4	(Morawetz & Waha 1985)
G. oliviformis	*Ehrendorfer 6400-1609*	28	4	(Sauer & Ehrendorfer 1984)
G. parvifolia[1]	*Morawetz 21-12381*	28	4	(Morawetz & Waha 1985)
G. peruviana	*Morawetz & Coêlho 21-24883*	28	4	(Morawetz & Waha 1985)
G. cf. *saffordiana*	*Ehrendorfer 6400-3711*	28	4	(Sauer & Ehrendorfer 1984)
G. salicifolia[1]	*Morawetz 21-11181*	28	4	(Morawetz & Waha 1985)
G. schlechtendaliana[5]	*Morawetz 11-27281*	28	4	(Morawetz & Waha 1985)
	Morawetz 15-17783			
	Morawetz 11-51083			
G. schomburgkiana	*Morawetz & Coêlho 11-19883*	28	4	(Morawetz & Waha 1985)
G. sellowiana	*Morawetz 21-7281*			
	Morawetz 21-8281	28	4	(Morawetz & Waha 1985)
G. sessiliflora[6]	*Morawetz & Coêlho 12-19883*			
G. silvatica[1]	*Morawetz 31-29181*	28	4	(Morawetz & Waha 1985)
G. sp. (sect. *Austroguatteria*)	*Gottsberger 12-12468*	28	4	(Sauer & Ehrendorfer 1984)
G. sp. (sect. *Pteropus*)	*Morawetz & Coêlho 17-23883*	28	4	(Morawetz & Waha 1985)
G. villosissima	*Morawetz 12-14381*	28	4	(Morawetz & Waha 1985)

[1] = *G. australis*; [2] = *G. punctata*; [3] = *G. guianensis*; [4] = *G. inundata*; [5] = *G. pogonopus*; [6] = *G. blepharophylla*.

Fig. 9 Karyotypes. a, b. *Guatteria pogonopus* Mart; c, d. *Guatteria friesiana* (W.A.Rodrigues) Erkens & Maas; e, f. *Guatteria campinensis* (Morawetz & Maas) Erkens & Maas. After Morawetz & Waha (1985; f. 5; reprinted with permission). a, b are completely contracted metaphasic chromosomes and c–f are prometaphasic ones. Note that the first pair is relatively big, also note the submetacentric pair nr. 6 and the telocentric chromosome nr. 7. — Scale bar = 5 µm.

of *Annonaceae* (Chatrou et al. 2012b) these hypotheses need to be reinvestigated.

Genome size has only been investigated in two *Guatteria* species: *G. hispida* and *G. pogonopus* (as '*G. schlechtendaliana*') (Bennett & Leitch 2012). Both species have a genome of about 1 Gbp, which is three times smaller than the largest *Annonaceae* genome reported (*Annona mucosa*, 2.9 Gbp) and almost double of the smallest one (*Friesodielsia obovata*, 420Mbp).

PALYNOLOGY

Only seven species of *Guatteria* have been studied for their pollen characteristics (*G. blepharophylla*, *G. campinensis*, *G. grandiflora*, *G. heteropetala*, *G.* aff. *inundata*, *G. megalophylla* and *G. oliviformis*). So far it shows that *Guatteria* has zonasulculate pollen in which the pollen wall has no coherent exine layer and consists primarily of intine (Walker 1971, Morawetz & Waha 1985). The exine consists exclusively of a loose network of globose and ellipsoidal sporopollenin granula embedded in the thick intine (Walker 1971, Morawetz & Waha 1985: f. 1d, Le Thomas et al. 1986: f. 15–16). This extreme reduction of the exine is autapomorphic and thus provides no evidence on relationships. Waha (1984) reports that the ring-like aperture has an unusual infolded form. This ring-like aperture should be considered as unique in *Annonaceae* in this respect (although ring-like apertures independently occur in very many angiosperm groups (Hesse & Zetter 2005)). It is not known if this aperture type is connected to a distinct mode of pollination. Doyle & Le Thomas (2012) suggest that the sulculus in the pollen of *Guatteria* and the African genus *Letestudoxa* might be homologous under a new interpretation of aperture states in *Annonaceae* (although this interpretation was equivocal in terms of parsimony in their study) but not under the more conventional interpretation (for a more detailed discussion on this issue see their paper).

The shape of the grains is ellipsoid to oblongoid to round or globular and they are 63–90 µm in size (Walker 1971), which is large for angiosperms but not for *Annonaceae*, which tend to have large pollen grains. Within *Annonaceae* this pollen size can be considered medium-sized (e.g., Doyle & Le Thomas 2012).

PHYTOCHEMISTRY

(A. Perez-Gavilan, Maastricht Science Programme, Maastricht University, Maastricht, The Netherlands)

Of the 2 500 species of *Annonaceae* only approximately 150 (in 41 genera) have been chemically investigated (Costa et al. 2009). A literature survey indicates that of these studies, only a limited number focuses on the determination of the complete chemical composition of the plant. Species of the genus *Guatteria* whose leave-derived essential oils have been screened via gas chromatography-mass spectrometry (GC-MS) for their full spectrum of chemical constituents include *G. costaricensis* (*Haber 8060*), *G. amplifolia* (*Bello 558*), *G. oliviformis* (*Bello 4153*) (Palazzo et al. 2009) and *G. pogonopus* (*Nascimento Prata 22793*) (Fontes et al. 2013). *Guatteria* species have been shown to contain a large diversity of chemical compounds which can be grouped into alkaloids, aliphatics, amino acids and proteins, and aromatic compounds (Leboeuf et al. 1982a).

An aliphatic subgroup of importance is terpenoids, which are found in an abundant number of *Guatteria* species, paralleling the findings in several other genus including *Annona*, *Asimina* and *Deeringothamnus* (Lima et al. 2004, Costa et al. 2008, Goodrich & Raguso 2009, Palazzo et al. 2009, Teichert et al. 2009, Maia et al. 2012, Fontes et al. 2013). Of more than 80 terpenoids isolated, both mono- and sesquiterpenes are the most common, as illustrated by studies of *G. blepharophylla* (*Webber 7340*), *G. friesiana* (*Webber 7341*) and *G. hispida* (*Webber 7707*) (Costa et al. 2008). In particular, α-and β-pinene, cariophyllene, germacrene D and bicyclogermacrene are present in large concentrations in many *Guatteria* species (Fontes et al. 2013). Terpenoids are associated with olfactory properties (Teichert et al. 2009).

A large variety of alkaloids, including benzylisoquinolines, bisbenzylisoquinolines, berbines, aporphinoids and saxoguattine (Leboeuf et al. 1982b) can be isolated from *Guatteria*. This is an unsurprising fact considering the rich alkaloidal content of the greater part of the family of *Annonaceae* (Cavé 1985). Over 150 different alkaloids have been isolated to date from *Annonaceae* species. For some older but still comprehensive reviews see Cavé (Cavé 1985, 1987, Cavé et al. 1989).

Many of the alkaloids found in the genus are related to isoquinolines (Castedo et al. 1991), and in particular, *Guatteria* is one of the six genera from which most *Annonaceae*-derived bisbenzylisoquinolines have been isolated (Aminimoghadamfarouj et al. 2011). Examples include guattegaumerine from *G. friesiana* (Voucher 7071 at IMEPLAM) (Dehaussy et al. 1983) and the methylcurines found in the bark of *G. megalophylla* (*Prance 13936*) (Galeffi et al. 1975).

Aporphines and oxoaporphines are another alkaloidal subgroup commonly found in *Guatteria*. Aporphines found in multiple *Guatteria* species include lysicamine: *G. friesiana* (*Webber 7341*), *G. blepharophylla* (*Webber 7340*), *G. saffordiana* (*Sobrevila s.n.*, sample kept in the herbarium of Universidad Simón Bolívar, Venezuela), *G. punctata* (as *G. chrysopetala*; collected in Litani, French Guiana and as *G. poeppigiana* (*Oliveira 148.872*) (Garbarino et al. 1984, Hocquemiller et al. 1984, Lima et al. 2004, Costa et al. 2009, 2013), liriodenine: *G. friesiana* (*Webber 7341*), *G. blepharophylla* (*Webber 7340*), *G. modesta* (2082-3), *G. goudotiana* (*Cabrera s.n.*, CUVC), *G. blepharophylla* (as *G. dielsiana*; *Rodrigues 2861*), *G. scandens* (*CM 844*, *H.J. 2452*), *G. punctata* (as *G. chrysopetala*; collected in Litani, Franch Guiana) and *G. amplifolia* (as *G. diospyroides*; voucher specimens deposited in FCME) (Ammar et al. 1979, Hocquemiller et al. 1983, 1984, Goulart et al. 1986, Castedo et al. 1991, Pérez-Amador et al. 2004, Costa et al. 2009, 2013) and isoboldine: *G. goudotiana* (*Cabrera s.n.*, CUVC), *G. lucens* (as *G. dumetorum*), *G. punctata* (as *G. chrysopetala;* collected in Litani, French Guiana) and *G. megalophylla* (as *G. melosma*; 80718) (Zabel et al. 1982, Hocquemiller et al. 1984, Castedo et al. 1991, Correa et al. 2006), among others. Furthermore, 7-alkylaporphinoids such as goudotianine from *G. goudotiana* (*Cabrera s.n.*, CUVC) are found exclusively within *Guatteria* (Castedo et al. 1991).

The essential oils from *Guatteria* species possess rich biological activities, and many have been tested for their cytotoxic or antibacterial/antimicrobial activities with mixed results (Costa et al. 2008, Palazzo et al. 2009, Bezerra et al. 2012, Britto et al. 2012, Fontes et al. 2013, Ferraz et al. 2014).

FLORAL BIOLOGY AND POLLINATION

(A.C. Webber, Departamento de Biologia, Universidade Federal do Amazonas, Manaus, AM, Brasil; and
G. Gottsberger, Botanischer Garten und Herbarium, Universität Ulm, Ulm, Germany)

Our present knowledge of floral biology and pollination of *Guatteria* comes principally from studies of species of Brazilian lowland and upland Atlantic forests as well as gallery forests in the Central Brazilian cerrado region (Gottsberger 1970) and the Brazilian Amazon forests (Webber 1996).

Floral biology

The pendent flower buds, even in very early stages, present open, extended petals and look like open functional flowers, but nevertheless are small and often greenish structures which in this non-functional stage expose the unripe stamens and carpels and continue to grow for weeks and even months until attaining their final size. The protogynous anthesis lasts for two days. One day before the onset of anthesis the petals curve over the flower centre forming with their base a closed, dark pollination chamber. Already in the morning of that day the petals start to curve and in the early evening hours the pollination chamber is formed.

The consistency and often also the colour of the petals change with the beginning of anthesis. In the morning of the first day of anthesis, with flowers already exhibiting the closed pollination chamber (Table 2), petals still have the hard consistency of pre-anthetic flowers, but during the day become soft. In several Amazonian species (e.g., *G. foliosa*) it was observed that petals became dry already at the end of this first day of anthesis; one exception observed was *G. megalophylla* in which the petals became darker but maintained their soft consistency. Atlantic forest species (e.g., *G. australis*, including *G. curvinervia*, *G. parvifolia* and *G. hilariana*) also were observed to maintain their more or less soft consistency of petals. Notable is the colour change of petals with the onset of anthesis. With exception of *G. australis* (as '*G. parvifolia*'), which from the bud stage to the anthetic flower stages maintained its brownish green petal colour, most other investigated Atlantic forest species showed a colour change from green to yellow and sometimes to brown. In the Amazon species *G. foliosa*, there is a change from bright green in the pre-anthetic stage to a darker green in the initial stage of anthesis and finally to brown in the late anthetic stage. *Guatteria megalophylla* petals change from greenish to yellowish or orange with colour deepening towards the end of anthesis.

The modification of the *Guatteria* flowers at anthesis with regard to their appearance (forming a closed pollination chamber), consistency (getting soft petals) and colour (changing from green to yellow, orange or brown), also concerns its strong floral scent emissions in the morning of the first day of anthesis in the pistillate stage.The fruity scent emissions (reminiscent of bananas, kaki, *Annona* and other usually very ripe or even already fermenting fruits) during the early hours of the pistillate stage probably consist mainly of esters and alcohols (see Jürgens et al. 2000, Teichert et al. 2011). In one species, *G. liesneri* in Manaus, the scent was disagreeable, reminiscent of a mixture of decaying bananas and cheese.

During the first day of anthesis, sometimes as early as 4:00 h or as late as 6:00 h, the scent emissions commence and in some species finish already as early as 10:30 h (e.g., *G. foliosa*) or as late as 17:00 h (e.g., *G. megalophylla*) or even 19:00 h (e.g., *G. liesneri* in Manaus) of the same day. The pistils already become receptive during the night before the beginning of the scent emissions and maintain receptivity until the end of the afternoon or the early evening of the first day of anthesis. After the first day in the pistillate stage the flowers do not anymore produce scent. One consequence of this fact is that flowers that are not visited in this stage cannot function as pollen donors. Flowers of other *Annonaceae*, which emit scent in the pistillate and staminate stages, can be pollen donors even when the flower visitors arrive only in the staminate stage, which is the case in species of *Anaxagorea* and *Xylopia* (Webber 1996) and *Annona* (Gottsberger 1999). During the following late night hours the stigmatic head detaches and between 5:30 and 7:00 h of the second day of anthesis all four investigated Amazon species of *Guatteria* were observed to shed their stamens and pollen. Stamens and pollen grains are first kept in the still closed pollination chamber, but with the dropping of the petals, stamens and pollen grains, between 6:00 and 7:00 h, the staminate phase of anthesis is over.

Flowers of *G. pogonopus*, studied in the northern Atlantic forests around Recife (Marcus Braun, unpubl. data), also were diurnal and lasted nearly 24 hours. The petals were completely joined and started to turn from light green to yellowish brown one day before anthesis. Scent production started at c. 6:30 – 7:30 h; the stigmas were also receptive at this time. The main pollinator attraction phase was during the morning hours until about mid-day, after which scent production was weak or stopped altogether. No scent was produced thereafter. On the following morning (5:30 – 7:00 h) the switch from the pistillate to the staminate stage took place abruptly: the anthers opened explosively, expanding in volume and expelling the stigmatic head. Almost immediately thereafter (i.e., during the following minute) the petals dropped. On rare occasions it was observed that pollen shedding was accompanied by petal dropping, but with the stigma still attached. The stigma was consequently covered with pollen, which may have resulted in occasional self pollination.

Flower visitors and pollinators

Flowers of *Guatteria* species are exclusively pollinated by relatively small beetles, which are attracted by the strong scent in the pistillate stage. They penetrate the pollination chamber and remain then inside it until the petals drop at the end of the staminate stage the next morning. Before leaving the pollination chamber they are eating pollen. The Atlantic forest species studied so far were visited and pollinated principally by small, flat *Nitidulidae* (*Colopterus truncatus* and other species of this genus), as well as *Staphylinidae* and occasionally *Chrysomelidae*. The pollinating beetles were small enough and able to enter the pollination chamber. *Coccinellidae*, *Curculionidae*, *Rutelidae* were found to be predators gnawing principally the petals and occasionally the soft stigmas.

In Amazonian species of *Guatteria* pollinating beetles also were *Nitidulidae*, *Staphylinidae* and *Chrysomelidae*. The presence of pollinating beetles was studied with more detail in Manaus (Table 3). In three of the four species studied (*G. foliosa*, *G. megalophylla* and *Guatteria* sp.), *Staphylinidae* were dominating over *Nitidulidae* (several *Colopterus* species). Only in *G. liesneri*, *Nitidulidae* were dominating over *Staphylinidae*. *Chrysomelidae* have to be considered only occasional pollinators and occurred only in low percentage amounts or could not be observed at all.

Table 2 Floral dimensions in cm (n = 10) and principal petal colour during anthesis in four Amazon *Guatteria* species.

Species	Ped	P	Poll (l × d)	Colour
G. foliosa	1.5–2.3	2.5–3.6	0.7–1.0 × 0.7–0.9	green
G. liesneri	1.5–2.3	2.5–3.5	0.7–1.0 × 0.7–0.9	green
G. megalophylla	0.4–1.1	2.9–3.5	0.9–1.1 × 1.0–1.2	orange
Guatteria sp.	1.5–2.4	2.7–3.7	0.7–0.8 × 0.9–1.1	yellowish green

Ped = flower peduncle; P = petal length; Poll = dimensions (length and diameter) of pollination chamber.

Table 3 Mean number of beetle individuals inside flowers of four Amazon *Guatteria* species.

Species	NF	N Beet	*Staphylinidae*	*Nitidulidae*	*Chrysomelidae*
G. foliosa	13	7.1 (± 4.6)	71 %	25 %	4 %
G. liesneri	09	7.3 (± 7.1)	88 %	6 %	6 %
G. megalophylla	08	11.1 (± 4.8)	69 %	30 %	1 %
Guatteria sp.	07	2.3 (± 0.8)	75 %	25 %	0 %

NF = number of flowers investigated; N Beet = mean number of beetles per flower ± SD.

The beetles approached the scenting flowers principally between 5:50 and 10:00 h in the morning of the pistillate stage, but eventually arrived also as late as in the afternoon of this first day of anthesis. Apparently attracted by the floral scent emissions, they show a zigzag-like flight, coming closer and closer to the source of scent and finally pose on the petals and penetrate the pollination chamber passing over the receptive stigmas. When carrying pollen the beetles cause pollination. Drosophilid flies were observed to oviposit on the external parts of petals without penetrating the pollination chamber and therefore cannot be considered pollinators. Although flowers of *Guatteria* species diminish and loose scent emissions along the pistillate stage of the first day of anthesis, the pollinating beetle inside the pollination chamber stay until the next morning. When the pollination chamber disintegrates by the dropping of petals the beetles are forced to leave and fly off. Being attracted by scenting pistillate stage flowers the pollen-carrying beetles cause pollination when penetrating the pollination chamber and crawling over the receptive stigmas.

Reproductive system

Most species of *Guatteria* bear on one and the same individual tree anthetic flowers in the receptive pistillate stage and at the same time others in the pollen providing staminate stage. The individual flower however is strongly dichogamous, which means that the two sexual stages are totally separated without any overlapping, so that self pollination of a flower is not possible (but see *G. pogonopus*). Although it was not tested by hand pollination if species are self-compatible or self- incompatible, the presence of pistillate and staminate stage flowers on one individual (e.g., in *G. foliosa* and *G. megalophylla*) would at least provide possibilities of geitonogamous pollen transfer. In another Amazonian species (*Guatteria* sp.) different individuals were observed which either had all flowers in the pistillate or the staminate stage. This is an indication that in this species, with trees having flowers in reciprocal stages, the sexual pattern of heterodichogamy eventually is given (for a similar situation in *Annonaceae* see *Annona mucosa* (as '*Rollinia jimenezii* var. *nelsonii'* in Murray & Johnson 1987 and *Anaxagorea prinoides* in Teichert et al. 2011). Further studies at the population level may indicate if and how far heterodichogamy occurs in *Guatteria*, which would be the case when one part of the population is observed to be in the pistillate stage and the other in the staminate stage and when the two reciprocal mating types occur in a population at a 1 : 1 ratio.

Conclusion

Only about 10 species of the genus *Guatteria* have been studied yet with regard to their floral biology and pollination. This is a relatively low percentage of species, considering that *Guatteria* is one of the largest genera of *Annonaceae* with c. 175 species. On the other hand, the biological characteristics of the few species studied in the Atlantic and Amazon forests are largely in accordance, so that we might not be totally wrong to assume that the floral ecology of the whole genus is quite conservative and that there is not much variation or diversification among the species.

One remarkable character is the long development of greenish, open, and for flower predators supposedly relative unattractive buds. Only one day before entering its protogynous anthesis, the flowers change radically. They change their form and close the petals and form a dark floral chamber. They then become attractive for insects, and both floral predators and pollinators are attracted. The petals become soft, emit a strong fruit-like scent during the pistillate stage, and effectively lure small beetles to enter the floral or pollination chamber. The beetles themselves probably normally live and oviposit on ripe and fermenting fruits. By emitting strong fruit-like scents, the dark, closed flowers appear to be fruit-imitating structures (Gottsberger 1970). In entering the chamber the beetles have to cross over the receptive stigmas and they then transfer pollen when coming from a staminate stage flower. Chrysomelid, Nitidulid and Staphylinid beetles, among a few others, are the principal pollinators. They remain in the dark floral chamber until the second morning of anthesis, when they are first alimented by pollen and then released with pollen grains sticking on their bodies.

What is varying in the pollination system of *Guatteria* is the final petal colour, which can be more greenish, yellow, orange or brown, the scent compounds apparently vary somewhat and imitate different fruits and it is quite possible that the pollinator species vary among the different *Guatteria* species. On the other hand, it appears that the scent emitting flowers of *Guatteria* are not very specifically attracting their pollinators. In one species, namely *G. megalophylla*, six different species alone of *Nitidulidae* (all belonging to the genus *Colopterus*) were attracted. The floral biology of the highly specialized flowers of *Guatteria* apparently attract a broad spectrum of more generalistic fruit beetles.

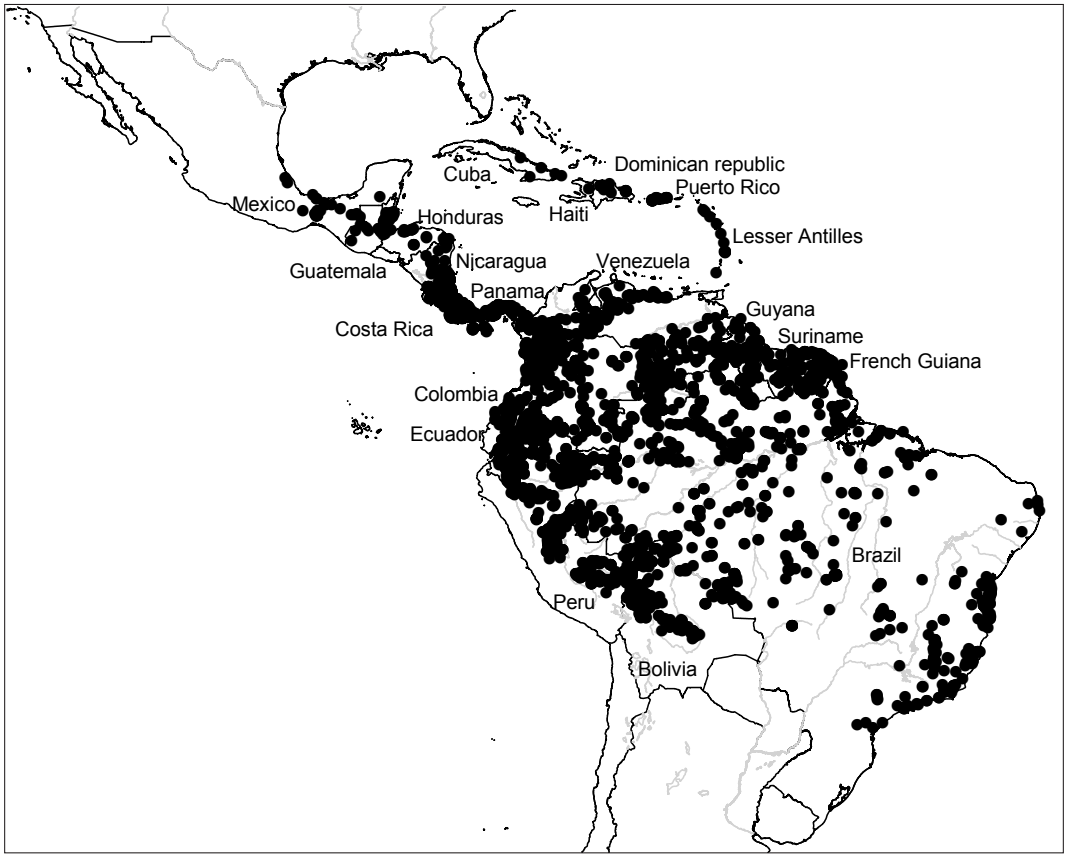
DISPERSAL

Mature monocarps in *Guatteria* are frequently black or dark purple often contrasting with red stipes. This, in combination with the fleshy fruit wall, seems a strong indication that fruits might be eaten by animals thus enabling endozoochorous seed dispersal.

The most detailed account came from Van Roosmalen (1985) who reported evidence of endozoochory by spider monkeys and howler monkeys, and by cotingids in *G. punctata* (as '*G. chrysopetala*'). There is a recent report of fruits of *G. alata* being eaten by the bird *Penelope purpurascens* ('Pava crestada') (*L. Martínez et al.1038*, Panama). There is also a report of quetzals eating fruits of *Guatteria* species in Monteverde, Costa Rica (Wheelwright 1983). However, the one species mentioned is unknown. No other observations on seed dispersal in *Guatteria* are known to us, neither in literature from field notes on herbarium labels.

DISTRIBUTION AND ECOLOGY — Map 1

Guatteria occurs in the Neotropics from Mexican state of Puebla (N20°00' W97°18') in the north to Bolivia and the S Brazilian state of Rio Grande do Sul (S29°26' W49°56') in the south. It has not been found so far in Argentina and Paraguay. In the Caribbean it is represented by two species, two in the Greater Antilles (*G. blainii* and *G. caribaea*) and one in the Lesser Antilles (*G. caribaea*), respectively. Several centres of distribution may be noted in the genus. By far the largest centre is the Western Amazon Basin, including Ecuador, Peru, Colombia, Venezuela, Western Brazil and Bolivia), with no less than 48 species. In Central America there are 33 species, while in northwestern and adjacent Central Colombia and Ecuador there are 16 species and in southeastern, eastern and northeastern Brazil 15 species. For the Guianas 37 species are counted falling into two categories: 22 species are endemic to that region, while 15 species have their main distribution in the Amazon Basin, but just reach the Guianas as well. There are only few species spanning the whole area of distribution or a major part of it, e.g., *G. tomentosa*, occurring all the way from Central America to SE Brazil, and *G. ucayalina* which is quite common in Central America but which is also found throughout the Amazon Basin and in Guyana. A third species, namely



Map 1 Distribution of *Guatteria* based on c. 6 850 georeferenced herbarium collections of almost all species.

G. hirsuta, is also widely spread, occurring in the western part of the Amazon Basin (with few collections from the eastern part), but also in Northern Venezuela and in the Pacific coast of Colombia. The fourth species is the most common one, namely *G. punctata* occurring all over tropical South America except for SE and E Brazil.

Geographical analysis for Guatteria

(for abbreviations see the list on page 18)

1. Greater Antilles (2 species) — blai, cari
2. Lesser Antilles (1 species) — cari
3. Central America and Mexico (33 species) — aber, acra, aeru, alat, alle, ampl, chir, cost, cras, dari, doli, dota, gale, graf, herr, jefe, luce, oliv, pacc, pana, pudi, rein, rost, rotu, sess, slat, taca, tala, tene, tome, ucay, vero, zamo
4. Central America to northwestern Colombia (2 species) — aber, dari
5. Central America to western part of South America (1 species) — ucay
6. Central America and large part of tropical South America (1 species) — tome
7. Northwestern and adjacent Central Colombia and Ecuador (16 species) — alta, arge, brep, carc, cras, cuat, elet, esme, goud, micr, nari, paci, pich, pitt, vall, veno
8. Central Colombia and Northern Venezuela (9 species) — anti, chas, novo, rufo, saff, spe2, syns, vene, veru
9. Guianas and adjacent Brazil and/or Venezuela (23 species) — alti, amap, ante, ayan, clus, cons, eles, flex, inte, leuc, minu, mont, obla, oure, paka, palu, pann, part, rich, rubr, scan, wach, woko
10. Amazon Basin and also in the Guianas (15 species) — aber, blep, citr, disc, foli, guia, lies, mayp, megp, meli, proc, punc, scho, scyt, subs
11. Western Amazon Basin (Ecuador, Peru, Colombia, Venezuela, Brazil and Bolivia) (49 species) — alba, arar, aren, atab, auya, beck, beni, bern, cast, chry, conf, cusc, decu, deli, denu, duod, dura, elat, erio, euge, flab, flag, frac, gent, grap, gris, hete, hirs, insc, japu, magu, megc, mode, obli, pacp, past, peru, rami, revo, rubo, sanc, scal, spec, spe3, stip, stpe, term, tric, tris
12. Central Amazon Basin (6 species) — cami, duck, elon, frie, hisp, stph
13. Amazon Basin (3 species) — inun, long, spe2
14. Throughout most parts of tropical South America (1 species) — punc
15. Eastern Amazon Basin (6 species) — crya, myri, odor, orix, poly, sabu
16. Southeastern, eastern and northeastern Brazil (15 species) — aust, came, cand, capi, emar, ferr, lati, macr, nota, olig, pogo, pohl, sell, stca, vill
17. Central Brazil (1 species) — rupe
18. Central Brazil and adjacent Amazonian Brazil (1 species) — rigi

Most species of *Guatteria* inhabit non-inundated rain forests, and only a few grow in periodically inundated rain forests (e.g., *G. heteropetala*, *G. inundata*). Few species are restricted to savannas (among others *G. campinensis*, *G. maypurensis*). The main bulk of *Guatteria* species occur in lowland forest, with just a handful of species occurring or reaching into montane or submontane forests (e.g., *G. goudotiana*, *G. oblongifolia*). The main altitudinal range is from 0–1500 m, with only few species exceeding this. The extremes are *G. oblongifolia* to 2900 m, *G. goudotiana*, reaching 3000 m, and *G. grandiflora* with one specimen collected at 3150 m! Many species are found on loamy, clayey or lateritic soils. Species growing on white sands are uncommon (e.g., *G. arenicola*, *G. atabapensis*, *G. maypurensis*).

TERMINOLOGY

Shape — For terms applying to shape we have consequently used the terminology recommended by the Systematics Association Committee for descriptive biological terminology (1962), Hickey (1979), Radford et al. (1974) and Stearn (1992).

Measurements — Measurements are mostly based on herbarium material. In cases where we used fresh or pickled material as well we indicated values obtained by including them between { }, e.g., 'fruit wall 0.1–0.2{–1} mm thick'.

Colour — Colour descriptions of leaves apply to herbarium material. Colours from fresh material (of petals and fruit) are referred to as 'in vivo'.

Inner floral parts — Measurements of carpels and torus are not included in this monograph.

TAXONOMIC TREATMENT

Guatteria

Guatteria Ruiz & Pav. (1794) 85; R.E.Fr. (1939) 291. — Lecto (selected by Hutchinson 1923): *Guatteria glauca* Ruiz & Pav. (= *Guatteria punctata* (Aubl.) R.A.Howard).

Cananga Aubl. (1775) 244, nom. rej. vs *Cananga* (A.DC.) Hook. & Thomson (1855), nom. cons. — Type: *Cananga ouregou* (= *Guatteria ouregou* (Aubl.) Dunal).

Heteropetalum Benth. (1861) 69. — Type: *Heteropetalum brasiliense* Benth. (= *Guatteria heteropetala* Benth.).

Guatteriopsis R.E.Fr. (1934) 108. — Lecto (selected by Fries 1959b): *Guatteriopsis sessiliflora* (Benth.) R.E.Fr. (= *Guatteria blepharophylla* Mart.).

Guatteria Ruiz & Pav. sect. *Acrantha* R.E.Fr. (1939) 303. — Type: *Guatteria terminalis* R.E.Fr.

Guatteria Ruiz & Pav. sect. *Austroguatteria* R.E.Fr. (1939) 304. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Asterantha* R.E.Fr. (1939) 318. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Microcalyx* R.E.Fr. (1939) 327. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Microphyllum* R.E.Fr. (1939) 332. — Type: *Guatteria pohliana* Schltdl.

Guatteria Ruiz & Pav. sect. *Cordylocarpus* R.E.Fr. (1939) 333. — Type: *Guatteria clavigera* R.E.Fr. (= *Guatteria australis* A.St.-Hil.).

Guatteria Ruiz & Pav. sect. *Trichoclonia* R.E.Fr. (1939) 335. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Stenophyllum* R.E.Fr. (1939) 354. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Leptophyllum* R.E.Fr. (1939) 372. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Macrophyllum* R.E.Fr. (1939) 375. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Guatteria* (1939) 383. — Lecto (selected by Hutchinson 1923): *Guatteria glauca* Ruiz & Pav. (= *Guatteria punctata* (Aubl.) R.A.Howard).

Guatteria Ruiz & Pav. sect. *Sclerophyllum* R.E.Fr. (1939) 390. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Macroguatteria* R.E.Fr. (1939) 395. — Lecto (selected by Fries 1959b): *Guatteria ferruginea* A.St.-Hil.

Guatteria Ruiz & Pav. sect. *Oligocarpus* R.E.Fr. (1939) 405. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Stenocarpus* R.E.Fr. (1939) 410. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Pteropus* R.E.Fr. (1939) 416. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Pycnantha* R.E.Fr. (1939) 431. — Type: *Guatteria elongata* Benth.

Guatteria Ruiz & Pav. sect. *Tylodiscus* R.E.Fr. (1939) 432. — Lecto (selected by Fries 1959b): *Guatteria chrysopetala* (Steud.) Miq. (= *Guatteria punctata* (Aubl.) R.A.Howard).

Guatteria Ruiz & Pav. sect. *Brachystemon* R.E.Fr. (1939) 454. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Cephalocarpus* R.E.Fr. (1939) 460. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Trichostemon* R.E.Fr. (1939) 470. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Dolichocarpus* R.E.Fr. (1939) 475. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Leiophyllum* R.E.Fr. (1939) 483. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Megalophyllum* R.E.Fr. (1939) 485. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Mecocarpus* R.E.Fr. (1939) 488. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Dichrophyllum* R.E.Fr. (1939) 509. — Type: *Guatteria discolor* R.E.Fr.

Guatteria Ruiz & Pav. sect. *Stigmatophyllum* R.E.Fr. (1939) 511. — Type: *Guatteria puncticulata* R.E.Fr. (= *Guatteria modesta* Diels).

Guatteria Ruiz & Pav. sect. *Chasmantha* R.E.Fr. (1939) 512. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Chasmantha* R.E.Fr. subsect. *Chasmantha* (1939) 513. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Chasmantha* R.E.Fr. subsect. *Verrucosae* R.E.Fr. (1939) 519. — Type: not designated.

Guatteria Ruiz & Pav. sect. *Chasmantha* R.E.Fr. subsect. *Grandiflorae* R.E.Fr. (1939) 523. — Type: *Guatteria grandiflora* Donn.Sm.

Guatteria Ruiz & Pav. sect. *Anomalantha* R.E.Fr. (1939) 524. — *Guatteria* Ruiz & Pav. subg. *Anomalantha* (R.E.Fr.) R.E.Fr. (1959b) 86. — Type: *Guatteria anomala* R.E.Fr. (= *Guatteria grandiflora* Donn.Sm.)

Guatteriella R.E.Fr. (1939) 540. — Type: *Guateriella tomentosa* R.E.Fr. (= *Guatteria trichocarpa* Erkens & Maas).

Trees or shrubs, very rarely lianas. Indument composed of simple, rarely tufted hairs or absent. Young twigs terete, rarely winged, densely to sparsely covered with appressed to erect hairs, soon becoming glabrous in many species. *Leaves* distichous, simple, entire, petiolate, estipulate; lamina mostly elliptic to ovate, chartaceous to coriaceous, sometimes verruculose, rarely scabridulous, upper side glabrous or less often sparsely to densely covered with appressed to erect hairs, lower side glabrous to densely covered with appressed to erect hairs, base acute, attenuate, cordate, or obtuse, rarely stem-clasping, apex acuminate to acute, very rarely obtuse to rounded, primary vein impressed, flat, rarely raised above, secondary veins distinct, sometimes indistinct, between 5 and 35 on either side of primary vein, angle of secondary veins with primary vein (30–)60–90° impressed to raised above, smallest distance between loops and margin 1–5(–10) mm, tertiary veins impressed to raised above, reticulate to percurrent. *Flowers* bisexual, 3-merous, commonly medium-sized, solitary or in 1–few-flowered inflorescences in axils of leaves or axils of fallen leaves, rarely terminal or terminal on lateral shoots, exceptionally inflorescences long-persisting and developing a varying number of successive flowers on older branches and in cauliflorous species and one flagelliflorous species; pedicels with mostly oblique articulation below the middle, with 2 bracts just below the articulation and mostly 4–6 bracts further down, without bracts above the articulation, bracts generally small, scale-like, soon falling, rarely one or more bracts persisting and foliaceous; pedicels and outer side of bracts, sepals and petals glabrous to densely covered with appressed to erect hairs; flower buds depressed to broadly ovoid, very rarely conical; sepals 3, valvate or reduplicate-valvate, free or connate at the base; petals 6, free, generally subequal, imbricate, much longer than the sepals, green, mostly maturing to cream or yellow in anthesis; stamens numerous, with very short filament, not septate, apex of connective discoid, papillate, glabrous, or rarely hairy; staminodes absent; carpels numerous, free, ovule 1, basal, stigma obovoid, discoid, or obconical, sometimes cup-shaped and grooved. Fruit apocarpous, consisting of numerous, indehiscent, stipitate, fleshy monocarps, stipes 5–50 mm long, sometimes absent or strongly reduced; seed 1, a rudimentary aril present, brown, surface smooth, pitted, rugulose, rugose, or transversely and longitudinally grooved, endosperm ruminations spiniform or lamellate.

Chromosome number — 2n = 28.

Distribution — About 177 species, all over the Neotropics except for Paraguay.

Habitat & Ecology — In non-inundated or rarely periodically inundated, lowland rain forest or sometimes submontane to montane forest, rarely in savannas. Generally at low elevations, but rarely reaching up to or over 3000 m.

Note — The genus is named after J.B. Guatteri, professor of Botany in Parma, Italy.

Keys

Guatteria, with few exceptions, is morphologically relatively homogeneous when compared to other annonaceous taxa. Also, there is great variation (or plasticity) in character states with much overlap as a result. Furthermore, *Guatteria* shows an extended period of flower development as contrasted with its short period of anthesis. Often ripe flowers show a marked increase in size and a change in colour (mostly lasting 1–2 days only). Unfortunately ripe flowers have still not been collected in many species. Inevitably, an attempt to construct a dichotomous key given the three factors mentioned above is going to result in several leads leading to the same species in many instances. Such a key is not only almost impossible to construct but also extremely frustrating to use. In our opinion, therefore, a synoptical key is to be preferred, like we did in the past in revisions of *Rollinia* (Maas et al. 1992) and *Duguetia* (Maas et al. 2003). For two smaller areas, however, viz. Central America and E and SE Brazil, in which only a limited number of species had to be treated, we decided to present a dichotomous key.

Synoptical key — The user may start with any number, depending upon the state of the material at hand. A useful lead is, of course, the entry devoted to geography. The species are represented by four-letter symbols (see below). Species mentioned in more than 1 lead are printed in *italics*. If there is a marked difference between the frequency ratio of character states, only the lead representing the one with the lowest value is printed in full. The alternate one is mentioned as 'vs' between parentheses.

aber = *G. aberrans*
acra = *G. acrantha*
aeru = *G. aeruginosa*
alat = *G. alata*
alba = *G. alba*
alle = *G. allenii*
alta = *G. alta*
alti = *G. alticola*
amap = *G. amapaensis*
ampl = *G. amplifolia*
ante = *G. anteridifera*
anti = *G. antioquensis*
arar = *G. araracuarae*
aren = *G. arenicola*
arge = *G. argentea*
atab = *G. atabapensis*
aust = *G. australis*
auya = *G. auyantepuiensis*
ayan = *G. ayangannae*
beck = *G. beckii*
beni = *G. beniensis*
bern = *G. bernardii*
blai = *G. blainii*
blep = *G. blepharophylla*
brev = *G. brevipetiolata*
came = *G. campestris*
cami = *G. campinensis*
cand = *G. candolleana*
capi = *G. capixabae*
carc = *G. carchiana*
cari = *G. caribaea*
cast = *G. castilloi*
chas = *G. chasmantha*
chir = *G. chiriquiensis*
chry = *G. chrysophylla*
citr = *G. citriodora*
clus = *G. clusiifolia*
conf = *G. confusa*
cons = *G. conspicua*
cost = *G. costaricensis*
crap = *G. crassipes*
crav = *G. crassivenia*
crya = *G. cryandra*
cuat = *G. cuatrecasasii*
cusc = *G. cuscoensis*
dari = *G. darienensis*
decu = *G. decurrens*
deli = *G. delicatula*
denu = *G. denudata*
disc = *G. discolor*
doli = *G. dolichopoda*
dota = *G. dotana*
duck = *G. duckeana*
duod = *G. duodecima*
dura = *G. dura*
elat = *G. elata*
eles = *G. elegans*
elet = *G. elegantissima*
elon = *G. elongata*
emar = *G. emarginata*
erio = *G. eriopoda*
esme = *G. esmeraldae*
euge = *G. eugeniifolia*
ferr = *G. ferruginea*
flab = *G. flabellata*
flag = *G. flagelliflora*
flex = *G. flexilis*
foli = *G. foliosa*
frac = *G. fractiflexa*
frie = *G. friesiana*
gale = *G. galeottiana*
gent = *G. gentryi*
goud = *G. goudotiana*
graf = *G. grandiflora*
grap = *G. grandipes*
gris = *G. griseifolia*
guia = *G. guianensis*
herr = *G. herrerana*
hete = *G. heteropetala*
hirs = *G. hirsuta*
hisp = *G. hispida*
insc = *G. insculpta*
inte = *G. intermedia*
inun = *G. inundata*
japu = *G. japurensis*
jefe = *G. jefensis*
lati = *G. latifolia*
leuc = *G. leucotricha*
lies = *G. liesneri*
long = *G. longicuspis*
luce = *G. lucens*
macr = *G. macropus*
magu = *G. maguirei*
mayp = *G. maypurensis*
megc = *G. megalocarpa*
megp = *G. megalophylla*
meli = *G. meliodora*
micr = *G. microcarpa*
minu = *G. minutiflora*
mode = *G. modesta*
mont = *G. monticola*
myri = *G. myriocarpa*
nari = *G. narinensis*
nota = *G. notabilis*
novo = *G. novogranatensis*
obla = *G. oblonga*
obli = *G. oblongifolia*
odor = *G. odorata*
olig = *G. oligocarpa*
oliv = *G. oliviformis*
orix = *G. oriximinae*
oure = *G. ouregou*
pacc = *G. pachycarpa*
paci = *G. pacifica*
pacp = *G. pachyphylla*
paka = *G. pakaraimae*
palu = *G. paludosa*
pana = *G. panamensis*
pann = *G. pannosa*
part = *G. partangensis*
past = *G. pastazae*
peru = *G. peruviana*
pich = *G. pichinchae*
pitt = *G. pittieri*
pogo = *G. pogonopus*
pohl = *G. pohliana*
poly = *G. polyantha*
proc = *G. procera*
pudi = *G. pudica*
punc = *G. punctata*
rami = *G. ramiflora*
rein = *G. reinaldii*
revo = *G. revoluta*
rich = *G. richardii*
rigi = *G. rigida*
rost = *G. rostrata*
rotu = *G. rotundata*
rubo = *G. ruboides*
rubr = *G. rubrinervis*
rufo = *G. rufotomentosa*
rupe = *G. rupestris*
sabu = *G. sabuletorum*
saff = *G. saffordiana*
sanc = *G. sanctae-crucis*
scal = *G. scalarinervia*
scan = *G. scandens*
scho = *G. schomburgkiana*
scyt = *G. scytophylla*
sell = *G. sellowiana*
sess = *G. sessilicarpa*
slat = *G. slateri*
spe1 = *G. sp. 1*
spe2 = *G. sp. 2*
spec = *G. spectabilis*
stca = *G. stenocarpa*
stpe = *G. stenopetala*
stph = *G. stenophylla*
stip = *G. stipitata*
subs = *G. subsessilis*
syns = *G. synsepala*
taca = *G. tacarcunae*
tala = *G. talamancana*
tene = *G. tenera*
term = *G. terminalis*
tome = *G. tomentosa*
tric = *G. trichocarpa*
tris = *G. trichostemon*
ucay = *G. ucayalina*
vall = *G. vallensis*
vene = *G. venezuelana*
veno = *G. venosa*
vero = *G. verrucosa*
veru = *G. verruculosa*
vill = *G. villosissima*
wach = *G. wachenheimii*
woko = *G. wokomungensis*
zamo = *G. zamorae*

KEY TO THE CENTRAL AMERICAN SPECIES

1. Plant cauliflorous or ramiflorous. — Costa Rica . . . . . 78. *G. herrerana*
1. Plant not cauliflorous or ramiflorous 2
2. Flowers or inflorescence terminal (some axillary flowers may also be present) 3
2. Flowers or inflorescence axillary 4
3. Pedicels 10–65 mm long; leaves 10–22 by 3–8 cm; petals 15–40 mm long; flowers often in 2–several-flowered inflorescences. — Mexico, Guatemala, Honduras. . . . . 74. *G. grandiflora*
3. Pedicels 5–12 mm long; leaves 5–8 by 2–3.5 cm; petals 7–9 mm long; flowers always solitary. — Panama . . . . . 2. *G. acrantha*
4. Young twigs densely covered with erect hairs 5
4. Young twigs covered with appressed hairs or glabrous 17
5. Leaf base cordate (sometimes obtuse in *G. pudica*) . . . 6
5. Leaf base acute, obtuse or attenuate (sometimes oblique in *G. tomentosa*) 7
6. Lower side of leaves covered with reddish brown, soft hairs, upper side glabrous except for the hairy primary vein; pedicels 10–35 mm long; flower buds obtuse; sepals 5–8 mm long. — Costa Rica. . . . . 129. *G. pudica*
6. Both sides of leaves covered with brown, stiff hairs; pedicels 10–50(–70) mm long; flower buds slightly pointed; sepals 6–13 mm long. — Central America, tropical South America . . . . . 163. *G. tomentosa*
7. Primary vein raised on the upper side of the leaves (but also slightly raised to flat above in *G. zamorae* and in *G. tala-mancana*); leaves narrowly oblong-elliptic. — Costa Rica, Panama . . . . . 34. *G. chiriquiensis*
7. Primary vein impressed to flat on the upper side of the leaves (leaves narrowly ovate to narrowly obovate, never oblong-elliptic) 8
8. Leaves verruculose 9
8. Leaves not verruculose 12
9. Sepals 15–20 mm long; monocarps 20–30 mm long; stipes of monocarps 2–3 mm long. — Costa Rica, Panama. . . . . 160. *G. talamancana*
9. Sepals 4–10 mm long; monocarps 5–16 mm long; stipes of monocarps 2–10 mm long. 10
10. Petioles 3–9 mm long; young twigs finally glabrous. — Panama . . . . . 175. *G. zamorae*
10. Petioles 0–7 mm long; young twigs covered with long-persisting hairs 11
11. Young twigs often zigzagging; monocarp 2.3–3 times longer than the stipes; monocarps 9–16 mm long, wall c. 0.5 mm thick. — Costa Rica, Panama . . . 110. *G. oliviformis*
11. Young twigs not zigzagging; monocarp 1.3–1.6 times longer than the stipes; monocarps 8–12 mm long, wall 0.2–0.3 mm thick. — Honduras, Nicaragua, Costa Rica, Panama, Colombia . . . . . 3. *G. aeruginosa*
12. Flower buds distinctly pointed (but see also *G. ucayalina*); petals brown to chocolate-coloured; leaves coriaceous. — Panama, Colombia, Brazil (Roraima) . . . . 1. *G. aberrans*
12. Flower buds obtuse; petals green to yellow; leaves chartaceous (sometimes coriaceous in *G. ucayalina*) 13
13. Sepals 2–5 mm long; petals canary yellow; leaves mostly greenish when dried. — Panama . . . . . 6. *G. allenii*
13. Sepals 5–13 mm long; petals differently coloured; leaves never greenish when dried 14
14. Sepals appressed to spreading, but finally reflexed; upper side of leaves mostly covered with erect hairs; flower buds slightly pointed. — Central America, tropical South America . . . . . 163. *G. tomentosa*
14. Sepals soon reflexed; upper side of leaves glabrous except for the hairy primary vein or covered with appressed hairs; flower buds obtuse 15
15. Tertiary venation of leaves mostly percurrent; stipes of monocarps 8–50 mm long; sepals 4–11 mm long. — Nicaragua, Costa Rica, Panama, tropical South America . . . . . 166. *G. ucayalina*
15. Tertiary venation of leaves reticulate; stipes of monocarps 3–20 mm long; sepals 4–7 mm long 16
16. Petioles 2–6 mm long; pedicels 30–60 mm long; monocarps 7–11 mm long; stipes 15–20 mm long. — Honduras, Costa Rica, Panama . . . . . 51. *G. dolichopoda*
16. Petioles 5–10 mm long; pedicels 15–30 mm long; monocarps 5–7 mm long; stipes 3–10 mm long. — Panama . . . . . 159. *G. tacarcunae*
17. Young twigs distinctly winged. — Costa Rica, Panama. . . . . 4. *G. alata*
17. Young twigs terete 18
18. Leaves mostly lengthwise folded when dried. — Panama . . . . . 86. *G. jefensis*
18. Leaves never folded when dried 19
19. Leaves distinctly rounded at the apex, densely verruculose. — Panama . . . . . 137. *G. rotundata*
19. Leaves acuminate or sometimes acute at the apex, sometimes verruculose 20
20. Leaf venation strongly raised on both sides; primary vein raised on the upper side. — Costa Rica . . . . . 42. *G. crassivenia*
20. Leaf venation never raised on both sides; primary vein flat to impressed on the upper side 21
21. Monocarps sessile or shortly stipitate (stipes up to 3 mm long). 22
21. Monocarps distinctly stipitate (stipes > 2 mm long) . . . 24
22. Leaves 18–33 by 5–10 cm, rather densely verruculose. — Panama . . . . . 150. *G. sessilicarpa*
22. Leaves 7–20 by 3–6 cm, not or sparsely verruculose on the lower side 23
23. Monocarps globose, 20–25 mm diam, wall 5–6 mm thick; pedicels 10–20 mm long. — Costa Rica . . . . . 113. *G. pachycarpa*
23. Monocarps narrowly ellipsoid, 10–14 by 4–8 mm, wall 1–1.5 mm thick; pedicels 3–7 mm long. — Costa Rica. . . . . 132. *G. reinaldii*
24. Monocarps distinctly beaked at the apex; petiole 15–20 mm long. — Costa Rica . . . . . 136. *G. rostrata*
24. Monocarps rounded to minutely apiculate at the apex; petiole mostly much smaller (except *G. slateri* 4–20 mm long) 25
25. Leaves verruculose . . . . . 170. *G. verrucosa*
25. Leaves not verruculose 26
26. Young twigs mostly zigzagging; secondary veins raised on the upper side of the leaves 27
26. Young twigs straight; secondary veins impressed to raised on the upper side of the leaves 29
27. Flowering pedicels 0–5 mm long; monocarps 3–5 times longer than the stipes; monocarps 15–17 mm long. — Costa Rica . . . . . 52. *G. dotana*
27. Flowering pedicels 5–32 mm long; monocarps 0.7–2.6 times longer than the stipes; monocarps 7–10 mm long 28

28. Monocarp 1.6–2.6 times longer than the stipes; stipes of monocarps 3–10 mm long; upper side of leaves glabrous. — Panama . . . . . 151. *G. slateri*
28. Monocarp 0.7–0.8 times longer than the stipes; stipes of monocarps 8–14 mm long; upper side of leaves with a hairy primary vein. — Costa Rica, Panama . . . . . 40. *G. costaricensis*
29. Leaves very small and narrow (7–12 by 2–3 mm). — Costa Rica . . . . . 161. *G. tenera*
29. Leaves generally much larger 30
30. Pedicels 30–75 mm long. — Panama, Colombia . . . . . 46. *G. darienensis*
30. Pedicels 7–50 mm long 31
31. Basal margins of leaves often revolute; leaf venation distinctly raised on the upper side. — Costa Rica, Panama . . . . . 91. *G. lucens*
31. Basal margins of leaves not revolute; leaf venation flat to impressed above, rarely slightly raised on the upper side 32
32. Seeds pitted; leaf venation often distinctly impressed above. — Throughout Central America and Mexico . . . . . 10. *G. amplifolia*
32. Seeds rugose; leaf venation flat to slightly raised above 33
33. Leaves 10–15 by 3–5 cm, secondary veins 8–15; monocarps 10–13 mm long; stipes of monocarps 9–17 mm long. — Mexico . . . . . 71. *G. galeottiana*
33. Leaves 13–26 by 5.5–12 cm, secondary veins 15–18; monocarps 7–10 mm long; stipes of monocarps 6–10 mm long. — Panama . . . . . 118. *G. panamensis*

KEY TO THE SE AND E BRAZILIAN SPECIES

1. Plant cauliflorous. — Bahia, Espírito Santo, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro . . . . 64. *G. ferruginea*
1. Plant not cauliflorous 2
2. Flowers or inflorescences terminal. — Minas Gerais . . . . . 104. *G. notabilis*
2. Flowers or inflorescences in axils of leaves and/or on leafless branchlets 3
3. Leaf apex rounded or emarginate 4
3. Leaf apex acuminate, acute, rarely obtuse to emarginate (see also *G. rupestris*, *G. tomentosa*) 5
4. Leaves verruculose, apex emarginate, tertiary veins inconspicuous; pedicels 15–30 mm long. — Espírito Santo . . . . . 60. *G. emarginata*
4. Leaves not verruculose, apex rounded, emarginate, or acute, tertiary veins conspicuous; pedicels 10–15 mm long. — Minas Gerais . . . . . 141. *G. rupestris*
5. Stipes of monocarps 0–3 mm long 6
5. Stipes of monocarps 4–30 mm long (see also *G. campestris* and *G. villosissima*) 7
6. Young twigs densely covered with erect hairs; pedicels 2–10 mm long; monocarps ellipsoid to globose, 6–13 mm long; seeds smooth. — Mato Grosso, Paraíba, Pernambuco . . . . . 147. *G. schomburgkiana*
6. Young twigs glabrous; pedicels 8–25 mm long; monocarps narrowly ellipsoid, 13–17 mm long; seeds rugose. — Espírito Santo . . . . . 29. *G. capixabae*
7. Monocarps narrowly ellipsoid 8
7. Monocarps globose or ellipsoid 9
8. Monocarps 18–25 mm long; stipes of monocarps 5–10 mm long. — Bahia . . . . . 153. *G. stenocarpa*
8. Monocarps 13–17 mm long; stipes of monocarps 2–4 mm long. — Espírito Santo . . . . . 29. *G. capixabae*
9. Monocarps globose; seeds not attached to the monocarp wall in herbarium material. — Alagoas, Bahia . . . . . 109. *G. oligocarpa*
9. Monocarps ellipsoid; seeds attached to the monocarp wall in herbarium material 10
10. Young twigs densely covered with erect hairs 11
10. Young twigs densely covered with appressed hairs or glabrous 16
11. Pedicels 60–120 mm long. — Bahia, Espírito Santo, Minas Gerais . . . . . 92. *G. macropus*
11. Pedicels 5–70 mm long 12
12. Leaf margins revolute 13
12. Leaf margins not revolute (see also *G. tomentosa*) . . 14
13. Flower buds obtuse; leaf margins revolute over the whole length; stipes of monocarps 3–4 mm long. — Ceará, Espírito Santo, Minas Gerais, Rio de Janeiro . . . . . 172. *G. villosissima*
13. Flower buds slightly pointed; leaf margins revolute at the base only or not revolute; stipes of monocarps 4–20 mm long. — Bahia, Espírito Santo, Minas Gerais . . . . . 163. *G. tomentosa*
14. Leaves 17–40 by 5–15 cm; stipes of monocarps 10–25 mm long. — Bahia, Espírito Santo, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro . . . . . 64. *G. ferruginea*
14. Leaves 5–15 by 1.5–4 cm; stipes of monocarps 2–6 mm long 15
15. Leaf base cordate, rarely obtuse. — Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro . . . . . 28. *G. candolleana*
15. Leaf base acute. — Bahia, Distrito Federal, Espírito Santo, Goiás, Mato Grosso, Minas Gerais, Pernambuco, Rio de Janeiro, São Paulo . . . . . 149. *G. sellowiana*
16. Leaves 13–35 by 4–13 cm. — Alagoas, Bahia, Ceará, Espírito Santo, Mato Grosso, Minas Gerais, Paraíba, Pernambuco . . . . . 125. *G. pogonopus*
16. Leaves generally much smaller (4–21 by 1.5–7 cm) . 17
17. Sepals connate, 10–20 mm long. — Minas Gerais, Rio de Janeiro . . . . . 87. *G. latifolia*
17. Sepals free or sometimes basally connate, 5–10 mm long 18
18. Stipes of monocarps 2–5 mm long. — Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro . . 26. *G. campestris*
18. Stipes of monocarps 5–30 mm long 19
19. Stipes of monocarps 5–9 mm long; sepals free or initially connate, 5–7 mm long. — Bahia, Espírito Santo, Minas Gerais . . . . . 126. *G. pohliana*
19. Stipes of monocarps 10–30 mm long; sepals free, 5–10 mm long. — Bahia, Espírito Santo, Goiás, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo . . . . . 17. *G. australis*

SYNOPTICAL KEY

1. ***Habit***
liana (vs trees or shrubs) — *beck*, *flex*, *frac*, scan, *syns*.
2. ***Young twigs zigzagging (vs straight)*** — alta, *cost*, dota, eles, frac, *goud*, *lati*, *oliv*, *slat.*
3. ***Young twigs***
covered with erect hairs — aber, aeru, alle, alta, alti, amap, anti, arar, ayan, *beck*, beni, bern, *brev*, cami, cand, carc, chir, chry, citr, *cuat*, *decu*, *deli*, disc, doli, duck, elet, *erio*, *esme*, *euge*, ferr, frie, grap, guia, herr, *hirs*, hisp, insc, inte, *lies*, macr, micr, minu, *mont*, nota, novo, obla, obli, oliv, oure, pann, part, *peru*, poly, proc, pseu, pudi, *punc*, *revo*, rich, rubo, rubr, rufo, rupe, *saff*, sanc, scho, sell,

stip, *stpe*, stph, taca, tala, tome, *tric*, *tris*, ucay, vene, vill, wach, zamo, spe2.

covered with appressed hairs — acra, alat, alba, ampl, ante, aren, arge, atab, aust, auya, *beck*, blai, blep, *brev*, came, cari, cast, chas, clus, conf, cost, crap, crav, crya, *cuat*, cusc, dari, *decu*, *deli*, denu, dota, duod, dura, elat, eles, elon, emar, *erio*, *esme*, *euge*, flab, flag, flex, foli, frac, gale, gent, goud, *graf*, gris, hete, *hirs*, inun, jefe, leuc, *lies*, long, luce, magu, *mayp*, megc, megp, meli, mode, *mont*, myri, nari, odor, olig, *orix*, pacc, paci, palu, pana, past, *peru*, pich, pitt, pogo, *pohl*, *punc*, rami, rein, *revo*, rigi, rost, rotu, *rupe*, sabu, *saff*, scal, scan, scyt, sess, slat, spec, *stpe*, subs, syns, tene, term, *tric*, *tris*, vall, *veno*, *vero*, veru.

glabrous — capi, cons, *graf*, japu, lati, *mayp*, *orix*, pacp, paka, *pohl*, *rupe*, stca, *veno*, *vero*, woko, spe1.

4. ***Petiole length***

0–5 mm — *aber*, acra, aeru, *alba*, *alle*, alta, alti, *ampl*, *anti*, arar, *aren*, *atab*, *aust*, auya, *beck*, beni, bern, *blai*, brev, *came*, cami, cand, *capi*, carc, cari, chir, *chry*, *citr*, *cons*, *cost*, crav, crya, cuat, *cusc*, *dari*, *decu*, deli, *denu*, *disc*, *doli*, *dota*, *duck*, *duod*, *dura*, *elat*, eles, elet, *elon*, emar, *erio*, esme, *euge*, *foli*, frac, *frie*, *gale*, *goud*, *graf*, grap, *gris*, *guia*, hirs, hisp, *insc*, *inte*, *inun*, *jefe*, *lati*, leuc, *lies*, long, *luce*, *macr*, magu, *mayp*, *meli*, *micr*, *minu*, *mode*, *mont*, myri, nari, nota, novo, *obla*, *obli*, odor, *olig*, *oliv*, *orix*, *oure*, *paka*, *pana*, part, *past*, *peru*, *pitt*, *pogo*, pohl, poly, *proc*, *pseu*, *pudi*, *punc*, rein, *rich*, *rigi*, rubo, rubr, *rufo*, rupe, *sabu*, *saff*, *sanc*, *scho*, *scyt*, *sell*, *sess*, *slat*, *spec*, *stip*, *stpe*, *stph*, *subs*, *syns*, *taca*, tala, tene, *term*, tome, *tric*, *tris*, *ucay*, *vall*, *vene*, vero, *veru*, *vill*, *wach*, *woko*, *zamo*, *spe1*, *spe2*.

6–10 mm — *aber*, *alat*, *alba*, *alle*, *ampl*, *anti*, *aren*, *arge*, *atab*, *aust*, *ayan*, *beck*, *blai*, *blep*, *came*, *capi*, *chas*, *chry*, *citr*, *clus*, conf, *cons*, *cost*, *crap*, *cusc*, *dari*, *decu*, *denu*, *disc*, *doli*, *dota*, *duck*, *duod*, *dura*, *elat*, *elon*, *erio*, *euge*, *ferr*, *flab*, flag, *flex*, *foli*, *frie*, *gale*, *gent*, *goud*, *graf*, *gris*, *guia*, herr, *hete*, *insc*, *inte*, *inun*, japu, *jefe*, *lati*, *lies*, *luce*, *macr*, *mayp*, *meli*, *micr*, *minu*, *mode*, *mont*, *obla*, *obli*, *olig*, *oliv*, *orix*, *oure*, *pacc*, *paci*, *pacp*, *paka*, *pana*, *pann*, *past*, *peru*, *pich*, *pitt*, *pogo*, *proc*, *pseu*, *pudi*, *punc*, *rami*, *revo*, *rich*, *rigi*, rotu, *rufo*, *sabu*, *saff*, *sanc*, *scan*, *scho*, *scyt*, *sell*, *sess*, *slat*, *spec*, *stca*, *stip*, *stpe*, *stph*, *subs*, *syns*, *taca*, *term*, *tric*, *tris*, *ucay*, *vall*, *vene*, *veno*, *veru*, *vill*, *wach*, *woko*, *zamo*, *spe1*, *spe2*.

> 10 mm — *alat*, *amap*, *ampl*, ante, *arge*, *ayan*, *blep*, cast, *clus*, *crap*, *denu*, *disc*, *elon*, *ferr*, *flab*, *flex*, *foli*, *gent*, *hete*, *inun*, *luce*, *mayp*, megc, megp, *olig*, *pacp*, *paci*, palu, *past*, *pitt*, *pogo*, *proc*, *punc*, *rami*, *revo*, rost, saff, scal, *scan*, *scyt*, *sess*, *slat*, *spec*, *stca*, *ucay*, *veno*.

5. ***Leaf surface***

verruculose — aeru, alat, arar, arge, *atab*, *auya*, blep, cand, *capi*, *chas*, crap, crav, crya, cuat, decu, *disc*, duod, dura, elet, emar, euge, *gent*, *goud*, graf, grap, gris, guia, hisp, insc, *japu*, long, *luce*, megc, meli, *mode*, nari, nota, novo, *obli*, oliv, paci, paka, *past*, peru, *pitt*, *rein*, *rigi*, rotu, sess, tala, *tene*, tric, vall, *veno*, vero, zamo, *spe1*.

scabridulous — ante, ayan, clus, cons, flex, frie, *inun*, japu, palu, scan, veru, wach.

smooth — all other species.

6. ***Leaves folded lengthwise (vs not folded)*** — *jefe*, *mayp*.

7. ***Leaf base***

cordate — *ampl*, *cami*, cand, *flab*, frie, *hirs*, *pudi*, *punc*, *scan*, *tome*, *vill.*

stem-clasping — *cami*, *long*, *tome.*

different — all other species.

8. ***Basal margins of leaves revolute*** — *ampl*, *anti*, *blai*, carc, cast, *duck*, emar, *goud*, *luce*, mode, nota, pacp, *past*, pudi, revo, rufo, rupe, *sess*, stip, *tala*, *tome*, vill.

9. ***Leaf apex***

rounded, truncate or obtuse — acra, *aren*, *cast*, *crap*, *dari*, *flag*, *gris*, *hete*, *meli*, *nota*, pacp, *rigi*, *rotu*, *rupe*, *term*, *tome*.

emarginate — *blai*, *clus*, emar, *rigi*, *rupe*, *tome*.

different — all other species.

10. ***Hairs on lower side of lamina (sometimes on large veins only)***:

appressed (to erect on large veins only) — aber, acra, alat, alba, alta, ampl, ante, aren, arge, atab, aust, auya, ayan, beck, *beni*, *bern*, *blai*, blep, *brev*, *came*, *capi*, cari, cast, *chas*, *citr*, clus, *conf*, *cons*, cost, *crap*, *crav*, crya, *cuat*, cusc, *dari*, *decu*, *deli*, *doli*, dota, duod, dura, elat, eles, elon, emar, *erio*, esme, *euge*, flab, flag, *flex*, foli, frac, frie, gent, *goud*, *graf*, gris, *guia*, *hete*, *hirs*, inte, inun, jefe, lati, leuc, lies, long, luce, *magu*, *mayp*, *mega*, megc, *meli*, *mode*, mont, myri, *nari*, *novo*, obla, *obli*, odor, *olig*, *orix*, *pacc*, *paci*, *paka*, pana, pann, past, peru, *pich*, *pitt*, *pohl*, *proc*, *pseu*, *punc*, rami, rein, *revo*, rigi, rost, rotu, *rubr*, rupe, *sabu*, *saff*, *sanc*, scal, *scho*, scyt, sell, sess, slat, spec, *stip*, stpe, *stph*, *subs*, syns, taca, tene, term, *tric*, *tris*, *ucay*, vall, *veno*, vero, *veru*, *spe1*, *spe2*.

erect all over — aeru, alle, alti, amap, anti, arar, *beni*, *bern*, *brev*, cami, *cand*, carc, chir, chry, *citr*, *crav*, *cuat*, *decu*, *deli*, disc, *doli*, duck, elet, *erio*, *ferr*, *graf*, grap, *guia*, herr, *hirs*, hisp, insc, *macr*, micr, minu, nota, *novo*, *obli*, oliv, oure, part, poly, *proc*, pudi, *punc*, *revo*, rich, rubo, *rubr*, rufo, *saff*, *sanc*, *scho*, sell, *stip*, tala, tome, *tric*, *tris*, *ucay*, *vene*, vill, zamo.

glabrous — *blai*, *came*, *cand*, *capi*, *chas*, *conf*, *cons*, *crap*, *dari*, denu, *euge*, *ferr*, *flex*, gale, gent, *goud*, graf, *hete*, *hirs*, japu, *lies*, *macr*, *magu*, *mayp*, *mega*, *meli*, *mode*, *nari*, *olig*, *orix*, *oure*, *pacc*, *paci*, pacp, palu, *pich*, *pitt*, pogo, *pohl*, *pseu*, *sabu*, scan, *sess*, slat, stca, *stph*, *subs*, *vene*, *veno*, *veru*, wach, woko, *spe1*, *spe2*.

11. ***Primary vein raised on upper side of lamina (vs impressed to flat)*** — *aeru*, *alat*, *alle*, alti, *aren*, *beni*, *chas*, *chir*, *citr*, *conf*, crav, *crya*, *deli*, *disc*, *dota*, gent, *gris*, *hete*, *hirs*, *nota*, *oliv*, pacc, *proc*, *slat*, *stpe*, *subs*, *tala*, *vene*, *vero*, *zamo*.

12. ***Marginal vein present (vs absent)*** — arar, *cami*, cuat, decu, elet, grap, guia, *insc*, *long*, megp, novo, veno, wach, woko.

13. ***Secondary venation indistinct (vs distinct)*** — *aren*, atab, clus, cons, crya, denu, doli, duck, elat, *elet*, *euge*, frac, frie, japu, leuc, macr, mayp, minu, mode, nari, nota, obla, olig, pacp, paka, past, pogo, pohl, rubo, spe1.

14. ***Number of secondary veins***

5–9 (vs ≥10) — acra, *alle*, *alti*, *aren*, *arge*, *aust*, *auya*, *ayan*, *blai*, *cand*, *capi*, *cari*, *clus*, *conf*, *cost*, *cusc*, *duck*, eles, *emar*, *euge*, *flex*, *foli*, *gale*, *graf*, *herr*, *hirs*, *leuc*, *lies*, *macr*, *magu*, *minu*, *odor*, *oliv*, *orix*, *paka*, part, *pohl*, *pudi*, *rein*, *rigi*, *rotu*, *rubr*, *rupe*, *scan*, *scho*, *slat*, *stpe*, *syns*, *taca*, *tala*, *term*, *tome*, *vene*, *vero*, *vill*, *woko*.

> 20 (vs ≤ 20) — *aber*, *aeru*, *alata*, *ampl*, *arar*, *aust*, *blep*, *cami*, *cons*, *crav*, *crya*, *cuat*, *decu*, *disc*, *ferr*, *flab*, *frie*, *grap*, guia, insc, *inun*, *lies*, *long*, *mega*, *nari*, novo, *paci*, *palu*, *punc*, rami, *revo*, *rufo*, *sabu*, *sanc*, *stca*, *stip*, *tric*, *ucay*, veno.

15. ***Distance between loops/marginal vein and margin ≥ 5 mm (vs ≤ 4)*** — *atab*, cari, *citr*, *conf*, *dari*, *decu*, *denu*, *duck*, *dura*, *elat*, *ferr*, *flab*, *flex*, *frie*, *goud*, *gris*, *guia*, *hisp*, *inun*, *lies*, *micr*, *novo*, *obli*, *orix*, *oure*, *past*, *pich*,

pitt, *pogo*, *proc*, *pudi*, *punc*, *rein*, *revo*, *rost*, *rubri*, *sabu*, *sanc*, *scan*, sess, *stip*, *subs*, *ucay*, *veno*, *veru*, *wach*, *spe1*.

16. ***Tertiary venation***
percurrent (vs reticulate) — alat, amap, cami, *chrys*, *crap*, *disc*, *dura*, *elat*, *eles*, *graf*, grap, guia, *herr*, insc, *inte*, megp, *meli*, novo, *obla*, *orix*, *oure*, *palu*, *pana*, *punc*, rami, *revo*, *rich*, *sabu*, *syns*, *taca*, *tene*, *tric*, *ucay*, *veno*.
indistinct (vs distinct) — alat, ante, arar, cons, *cuat*, *dari*, decu, dura, elat, elon, emar, frie, long, megp, mode, nota, novo, obla, oliv, orix, palu, pana, past, pohl, punc, scal, *scan*, stca, subs, tala, *wach*.

17. ***Flower position***
terminal — acra, *blai*, *graf*, nota, term.
in leaf axils — aber, *aeru*, *alba*, alle, alta, alti, amap, *ampl*, ante, anti, *arar*, aren, arge, atab, *aust*, auya, ayan, beck, beni, bern, *blai*, blep, *brev*, came, *cami*, cand, capi, carc, *cari*, cast, *chas*, *chir*, *chry*, *citr*, clus, conf, *cons*, cost, *crap*, crav, *crya*, cuat, *cusc*, dari, decu, deli, *denu*, disc, doli, *dota*, duck, *duod*, *dura*, *elat*, elet, *elon*, emar, *erio*, esme, euge, *ferr*, *flab*, *flex*, foli, frac, frie, gale, *gent*, goud, *graf*, grap, *gris*, *guia*, hete, *hirs*, hisp, *insc*, inte, *inun*, *japu*, *jefe*, lati, *lies*, *long*, luce, macr, magu, *mayp*, megc, *megp*, *meli*, *micr*, minu, *mode*, *mont*, *myri*, nari, *obla*, obli, odor, olig, oliv, *orix*, *oure*, pacc, *paci*, *pacp*, *paka*, *palu*, *pana*, *pann*, *part*, *past*, peru, pich, pitt, pogo, pohl, *poly*, *proc*, pseu, pudi, *punc*, *rami*, rein, *revo*, *rich*, rigi, *rost*, rotu, *rubo*, rubr, *rufo*, rupe, sabu, *saff*, *sanc*, *scho*, *scyt*, sell, sess, slat, spec, stca, stpe, stph, *stip*, *subs*, *syns*, taca, tala, tene, *tome*, tric, tris, *ucay*, *vall*, vene, *veno*, vero, veru, vill, *wach*, woko, zamo, spe1, spe2.
on leafless branchlets — *aeru*, alat, *alba*, *amap*, *ampl*, *arar*, *aust*, *blai*, *brev*, *cami*, *cari*, *chas*, *chry*, *citr*, *crap*, *crya*, *cusc*, *denu*, *dota*, *duod*, *dura*, *elat*, eles, *elon*, *erio*, *ferr*, *flab*, *flex*, *gent*, *gris*, *guia*, *herr*, *hirs*, *insc*, *inun*, *japu*, *jefe*, leuc, *lies*, *long*, *mayp*, *mega*, *meli*, *micr*, *mode*, *mont*, *myri*, *obla*, *orix*, *oure*, *paci*, *pacp*, *paka*, *palu*, *pana*, *pann*, *part*, *past*, *poly*, *proc*, *punc*, *rami*, *revo*, *rich*, *rost*, *rubo*, *rufo*, *saff*, *sanc*, *scan*, *scho*, *scyt*, *stip*, *subs*, *syns*, *tome*, *ucay*, *vall*, *veno*, *wach*.
plant cauliflorous — *cons*, *ferr*, *herr*, *long*, novo, *scan*, scal.
plant flagelliflorous — flag.

18. ***Flowers***
solitary (exceptionally ≥ 2) — acra, aeru, alat, alba, alta, alti, *ampl*, ante, arar, aren, arge, aust, auya, beck, beni, bern, blai, cand, capi, cast, chry, clus, conf, cons, cost, crav, cuat, cusc, decu, deli, denu, doli, dota, dura, elat, eles, emar, *erio*, esme, euge, *ferr*, flex, foli, frac, gale, *graf*, grap, guia, hete, hirs, hisp, insc, inte, inun, lati, leuc, *long*, macr, magu, mayp, megp, meli, micr, minu, mont, myrio, nari, obla, obli, odor, olig, oliv, oure, pacc, paci, paka, palu, part, past, peru, pich, pohl, proc, pudi, rigi, rotu, rubo, rubr, rupe, scho, sell, sess, slat, stca, stpe, stph, taca, tala, tene, term, tome, tric, tris, vall, vene, vero, veru, vill, woko, zamo.
1–≥ 2-flowered inflorescences — aber, alle, amap, *ampl*, anti, atab, ayan, blep, brev, came, cami, carc, cari, chas, chir, citr, crap, crya, dari, *disc*, duck, duod, elet, *erio*, *ferr*, flab, frie, gent, goud, gris, herr, japu, jefe, lies, *long*, luce, mode, nota, orix, pacp, pana, pann, pitt, pogo, poly, pseu, punc, rami, rein, revo, rich, rost, rufo, sabu, saff, sanc, scyt, spec, stip, subs, ucay, veno, wach, spe1, spe2.
2–∞ — *disc*, elon, *erio*, *ferr*, flag, *graf*, *long*, novo, scal, scan.

19. ***Length of pedicels (flowering, fruiting)***
≤ 10(–15) mm — acra, *alle*, amap, *ampl*, *ante*, arar, *aren*, *arge*, atab, auya, *ayan*, *blep*, *came*, *cami*, *capi*, *cari*, *chas*, *citr*, *conf*, cons, *cost*, crav, crya, *denu*, *disc*, *dota*, duck, *duod*, *dura*, *elat*, elon, *flex*, frie, *gale*, gent, *goud*, *graf*, *hete*, *hirs*, hisp, *inte*, *jefe*, leuc, *lies*, *luce*, *magu*, *megp*, *meli*, *minu*, *mode*, *mont*, *nota*, *obla*, *obli*, *olig*, *oliv*, orix, *oure*, *pacc*, *palu*, *pann*, *past*, *peru*, *pogo*, *pohl*, *poly*, *pseu*, *pudi*, *punc*, rein, *revo*, *rich*, rotu, *rufo*, *rupe*, *sabu*, *saff*, scho, *scyt*, *sell*, *sess*, *stip*, *stph*, subs, *syns*, *tene*, *term*, *tome*, *tric*, *ucay*, *veno*, *vero*, *vill*, *wach*, *zamo*, *spe1*, *spe2*.
≥ 30 mm — alta, *ampl*, *aust*, beni, *blai*, *blep*, brev, *cand*, *chir*, *chry*, *crap*, *cuat*, cusc, dari, *decu*, doli, *dura*, *elet*, *emar*, *ferr*, *flag*, *flex*, *foli*, *gale*, *goud*, *graf*, grap, *gris*, *guia*, *hirs*, *insc*, *inun*, japu, *jefe*, *lati*, *lies*, *long*, *luce*, macr, *magu*, *mayp*, megc, *micr*, *nari*, novo, *obli*, *oliv*, *paci*, paka, *pana*, part, *pich*, *pitt*, *pogo*, *pohl*, *pudi*, *punc*, *rami*, *rigi*, *rost*, *rubo*, *rubr*, *rufo*, *saff*, *sanc*, *scal*, *scan*, *slat*, *spec*, *stca*, stpe, *taca*, *tala*, *tome*, *tris*, *ucay*, *vall*, *vene*, *vill*, *woko*, *zamo*.
10–30 mm — all other species.

20. ***Flower buds***
pointed or acute (vs obtuse; unknown in some species) — aber, amap, aren, ayan, *blai*, chry, disc, doli, guia, hirs, megp, palu, pann, *punc*, *rami*, rubo, rubr, sanc, *scyt*, tome, *ucay*.
conical (vs depressed to broadly ovoid or triangular-ovoid; unknown in some species) — aber, amap, frie, hete.

21. ***Sepal length***
>10 mm long (vs ≤10 mm long) — *aber*, alat, *ampl*, arar, *areu*, chry, *cuat*, *decu*, *disc*, *ferr*, frie, *graf*, grap, *guia*, *hirs*, *hisp*, *insc*, lati, *macr*, megp, nota, novo, *pann*, *past*, *pitt*, *punc*, *rost*, *sanc*, *spec*, tala, *tome*, *tric*, *ucay*, *vill*.

22. ***Petals unequal (vs subequal)*** — frie, hete, rost.

23. ***Petal colour (but notice that the flower colour of many species is still unknown)***
brown to black — aber, cami, *foli*, *mayp*, *sanc*, *syns*, *veno*.
reddish to purple — *cuat*, *flab*, *hete*, *luce*, *megp*, *nota*, *obli*, *pann*, *past*, peru, *revo*, *sanc*, *scho*, *stip*, *vill*.
grey to black — goud, term.
orange — *carc*, *luce*, *megp*, *oure*, *rubr*, *vill*.
different colours — all others, including the species for which the flower colour is still unknown).

24. ***Stamens with connective shield densely hairy (vs glabrous, papillate or [thinly] hairy)*** — amap, anti, citr, duck, poly, scho, stip.

25. ***Monocarp size***
< 10 mm (vs ≥ 10 mm) — *acre*, *aeru*, *alle*, *alta*, *aren*, *atab*, *aust*, *beck*, beni, *blai*, *cand*, *cast*, *chir*, *cons*, *cost*, *crya*, *cuat*, *dari*, deli, denu, *doli*, duck, eles, elet, esme, *ferr*, *flab*, *flag*, *foli*, *hirs*, inte, *lati*, leuc, *lies*, *luce*, magu, *mayp*, *micr*, *minu*, *mode*, mont, myri, nari, *obli*, *oliv*, *oure*, *pana*, *part*, *pitt*, *pohl*, *proc*, *pudi*, *punc*, rich, *rigi*, *rubo*, rubr, *rufo*, *rupe*, *sabu*, *saff*, scho, *scyt*, sell, *slat*, *stip*, *stpe*, *syns*, *taca*, *tome*, *ucay*, vall, *vene*, vill, wach, *zamo*.
> 20 mm long — *alat*, ante, *ayan*, *blep*, *chry*, *clus*, *conf*, *decu*, *disc*, *frie*, *graf*, *guia*, *hete*, *hisp*, *inun*, *long*, megc, *megp*, *meli*, pacc, *peru*, rami, *scal*, *sess*, *stca*, *tala*, *tric*.
different length — all other species.
unknown — alba, alti, auya, brev, crav, elon, emar, erio, frac, odor, poly, rufo, spec, stph, tene, tris.

26. ***Monocarps < 10*** — acra, *alat*, ante, arar, ayan, cand, capi, *cari*, cast, *chry*, citr, *clus*, frie, *graf*, *hete*, *leuco*, *orix*, paka, part, pseu, *punc*, rein, *rost*, *scho*, *sess*, *stca*, *stip*, *subs*, *woko*, *spe2*.

27. ***Monocarp shape***
fusiform (vs differently shaped) — hisp, inun.
narrowly oblongoid (vs differently shaped) — mayp.

28. ***Thickness of monocarp wall***
1–2 mm — alat, ante, arge, *cami*, cast, chry, clus, *crap*, *decu*, *disc*, *duck*, *duod*, euge, *gent*, *guia*, *insc*, mega, megp, meli, *mode*, nota, olig, *pann*, *past*, *pich*, *pogo*, *punc*, rein, *scal*, sess, stca, tric, *vero*.
> 3 mm — pacc, *vero*.
unknown — alba, alti, auya, beni, brev, crav, elon, emar, erio, euge, frac, graf, odor, pana, poly, spec, stph, tene, tris, *vero*, woko, spe2.
< 1 mm — all other species.

29. ***Monocarp indument***
densely covered with appressed hairs — amap, lies (but soon glabrous!), tric.
densely to rather densely covered with erect hairs ('hirsute') — *arar*, *decu*, hisp, *rubo*.
densely covered with erect hairs ('velutinous') — cami, *nota*, *pann*, stip.
rather densely covered with appressed and erect hairs — beni.

30. ***Stipe length***
0–4 mm — acra, *alat*, *alle*, aren, *arge*, *atab*, beni, blai, *came*, *cami*, capi, *cari*, *chas*, citr, *clus*, *conf*, cons, *crap*, crya, *cuat*, cusc, denu, *disc*, *dota*, duck, *duod*, *elet*, *esme*, frie, *graf*, gris, *guia*, hete, *inun*, *jefe*, magu, *mayp*, *megp*, nota, *obli*, *oliv*, pacc, *paci*, *pacp*, paka, past, rein, *revo*, *rigi*, *rost*, rotu, rubo, rufo, *rupe*, *sabu*, *sanc*, scho, sess, *slat*, *subs*, *syns*, *taca*, tala, term, *tome*, *tric*, *vene*, *vero*, veru, vill, *wach*.
> 20 mm — *alat*, *ampl*, *aust*, *carc*, *elat*, *ferr*, *foli*, herr, *hirs*, *inte*, *lati*, *lies*, *micr*, *myri*, *olig*, *our*, *pann*, *proc*, *punc*, *rubr*, *saff*, *scal*, *scyt*, *ucay*, *woko*.
different length — all other species.
unknown — alba, alti, auya, brev, crav, elon, emar, erio, frac, odor, poly, rufo, spec, stph, tene, tris.

31. ***Seed surface***
smooth — *aber*, aren, *ayan*, bern, *blai*, *chir*, citr, disc, duck, *euge*, *flex*, foli, *minu*, *mode*, *olig*, *pann*, *pogo*, *punc*, *revo*, *rubr*, *rupe*, scho, *scyt*, stip, *syns*, *term*, *ucay*.
pitted — *acra*, *aber*, ampl, anti, arge, *atab*, *ayan*, beck, *came*, cand, *cari*, *chir*, *cons*, crya, *cusc*, dari, *denu*, doli, *dota*, elat, *eles*, *euge*, ferr, *flab*, *goud*, herr, *hete*, *hirs*, inte, *inun*, jefe, lati, *lies*, luce, macr, *magu*, mayp, micr, *minu*, *mode*, *mont*, myri, nari, obla, *obli*, *olig*, *oure*, *paci*, *pann*, part, *past*, *pich*, *pogo*, *pohl*, *proc*, pudi, *punc*, rein, *revo*, *rich*, rami, rigi, *rost*, *rubr*, *rupe*, sabu, *saff*, *sanc*, *scyt*, sell, *sess*, *slat*, *stpe*, *syns*, *tala*, *term*, tome, *ucay*, *vall*, vill, *wach*, woko, spe1.
transversely grooved — *ante*, *atab*, *camp*, *cons*, *cost*, deli, *dota*, *eles*, *esme*, *flab*, *flex*, frie, *hete*, *hirs*, *leuc*, *lies*, *mont*, *oure*, *paci*, *past*, *pich*, *pohl*, *proc*, *punc*, *rich*, *rost*, *scyt*, *sess*, *slat*, *stpe*, *zamo*.
longitudinally grooved — *acra*, *blai*, *camp*, *dura*, *inun*, *pacp*, *wach*.
rugulose — alat, *ante*, aust, *blep*, *came*, *camp*, carc, *clus*, *cons*, *cost*, *duod*, *dura*, elet, *goud*, *graf*, *guia*, *hisp*, leuc, *long*, *magu*, *minu*, nota, *obli*, *pacp*, paka, palu, rubo, *saff*, *sanc*, *tala*, *vall*, vene, veno.
rugose — *acra*, aeru, alle, alta, amap, *blep*, capi, chry, crap, cuat, *denu*, duod, *esme*, flag, gale, *gent*, *graf*, grap, gris, megc, *megp*, oliv, orix, pacc, pana, pitt, *punc*, rotu, rufo, *subs*, vero, *zamo*.
longitudinally and transversely grooved — arar, *blai*, *blep*, *cami*, *cari*, conf, decu, *gent*, *guia*, *hisp*, insc, japu, *long*, *megp*, novo, peru, scal, scan, stca, *subs*, tric, veru.
unknown — alba, alti, brev, cast, chas, crav, elon, emar, erio, frac, meli, odor, pana, poly, spec, stph, taca, tene, tris, spe2.

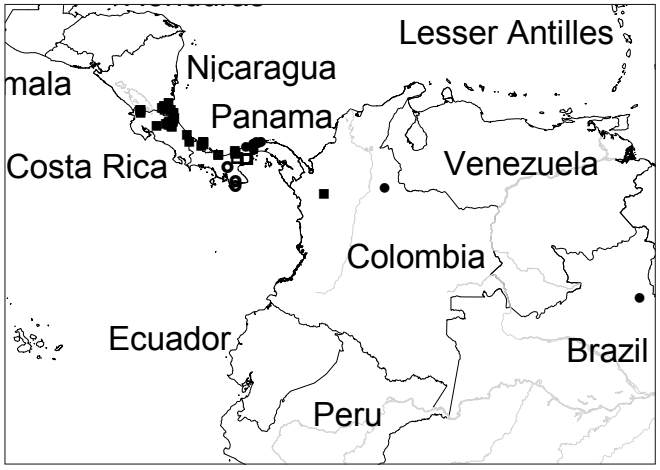
32. ***Distribution***
Antilles — blai, cari.
Central America and Mexico — *aber*, acra, aeru, alat, alle, ampl, chir, cost, crav, *dari*, doli, dota, gale, graf, herr, jefe, luce, oliv, pacc, pana, pudi, rein, rost, rotu, sess, slat, *taca*, tala, tene, *tome*, *ucay*, vero, zamo.
Pacific Colombia and Pacific Ecuador — *aber*, alta, anti, *arge*, *brev*, carc, *citr*, *crap*, *cuat*, *dari*, elet, esme, *goud*, *hirs*, micr, nari, paci, *pich*, pitt, *punc*, *taca*, *tome*, *ucay*, vall, veno.
Central Colombia and Central Ecuador — *arge*, chas, *crap*, *cuat*, *dari*, *goud*, *guia*, *hirs*, *lies*, *megp*, novo, *punc*, rufo, *stip*, *subs*, *tome*, *ucay*, *veru*.
Northern Venezuela — bern, *foli*, *hirs*, *mayp*, *punc*, saff, *scho*, *subs*, *ucay*, vene, *veru*.
Guianas (including adjacent regions in Brazil and Venezuela) — alti, *ante*, ayan, *blep*, *citr*, clus, cons, *disc*, eles, *flex*, *foli*, *guia*, inte, leuc, *lies*, *mayp*, *megp*, *meli*, minu, *mont*, obla, oure, paka, palu, *pann*, part, *proc*, *punc*, *rich*, *rubr*, *scan*, *scho*, *scyt*, *subs*, *ucay*, *wach*, woko.
Western Amazon Basin (W of Manaus) — alba, arar, aren, atab, auya, beck, beni, *blep*, brev, cast, chry, *citr*, conf, cusc, decu, deli, denu, *disc*, duod, *dura*, elat, erio, euge, flab, flag, *flex*, *foli*, frac, gent, *goud*, grap, gris, *guia*, hete, *hirs*, insc, *inun*, japu, *lies*, *long*, magu, *mayp*, megc, *megp*, *meli*, mode, *mont*, obli, pacp, *past*, peru, *proc*, pseu, *punc*, rami, revo, *rigi*, rubo, *rubr*, sanc, scal, *scan*, *scho*, *scyt*, spec, *stip*, stpe, stph, *subs*, term, *tome*, *tric*, tris, *ucay*, *spe1*, spe2.
Central Amazon Basin — *blep*, cami, *citr*, duck, elon, frie, hisp, *inun*, *lies*, *long*, *past*, *scyt*, *subs*.
Northern Brazil (Amapá, Roraima) — *aber*, amap, *ante*, *blep*, *crya*, *guia*, *lies*, *mayp*, *megp*, *pann*, *punc*, *rich*, *scan*, *scho*, *tric*, *wach*.
Eastern Amazon Basin (E of Manaus) — *blep*, *citr*, *crya*, *ferr*, *foli*, *guia*, *hirs*, *inun*, *lies*, *long*, *megp*, myri, odor, orix, poly, *proc*, *punc*, *rigi*, sabu, *scan*, *scho*, *scyt*, *subs*, *spe1*.
Northeastern Brazil (Alagoas, Ceará, Maranhão, Paraiba, Pernambuco, Piauí) — *citr*, *mode*, *olig*, *pogo*, *punc*, *scan*, *scho*.
Eastern Brazil (Bahia, Espirito Santo) — *aust*, *came*, *cand*, capi, emar, *ferr*, *macr*, *nota*, *olig*, *pogo*, *pohl*, *sell*, stca, *tome*, *vill*.
Central Brazil (Goiás, Mato Grosso, Minas Gerais) — *aust*, *blep*, *came*, *cand*, *dura*, *ferr*, *foli*, *lati*, *macr*, *mayp*, *nota*, *pogo*, *pohl*, *punc*, *rigi*, rupe, *scyt*, *sell*, *tome*, *vill*.
Southeastern Brazil (Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo) — *aust*, *came*, *cand*, *ferr*, *lati*, *sell*, *vill*.

33. ***Elevation***
above 2000 m (vs 0–2000 m) — *aren*, *carc*, *crap*, *frac*, *goud*, *gris*, *obli*, *oliv*, *past*, *punc*, *slat*, *syns*, *term*.

1. *Guatteria aberrans* Erkens & Maas — Map 2

Guatteria aberrans Erkens & Maas in Erkens et al. (2006) 201, t. 1, f. 1. — Type: *Maas et al. 9570* (holo U; iso INB, K, MO, PMA, SCZ), Panama, Colón, Santa Rita Ridge, Parcela 31 of CTFS, 250 m, 9 June 2004.

Tree 8–25 m tall, 10–30 cm diam; young twigs densely covered with erect, curly, brown hairs, soon glabrous. *Leaves*: petiole 5–10 mm long, 2–3 mm diam, decurrent as prominent ridge in young twigs; lamina narrowly elliptic, sometimes narrowly ovate, 15–32 by 4–9.5 cm (leaf index 2.9–3.7), coriaceous, not verruculose, shiny, dark blackish brown to grey above, brown to pale brown below, sparsely covered with appressed hairs above, soon glabrous, sparsely covered with appressed hairs



Map 2 Distribution of *Guatteria aberrans* (●), *G. acrantha* (⊙), *G. aeruginosa* (■) and *G. allennii* (□).

below, base obtuse, extreme base sometimes slightly attenuate, apex acuminate (acumen 10–20 mm long), primary vein flat to slightly impressed above, secondary veins distinct, 15–22 on either side of primary vein, raised above, smallest distance between loops and margin 3–4 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2(–3)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 7–20 mm long, 1–2 mm diam, fruiting pedicels 2–3 mm diam, densely covered with erect, curly, brown hairs (to rather densely covered with appressed hairs in the Roraima specimen), articulated at c. 0.2 from the base, bracts 4–6, soon falling, not seen; flower buds conical to ovoid, distinctly pointed; sepals free, triangular to broadly triangular, 7–12 by 5–8 mm, spreading but soon becoming completely reflexed, outer side densely covered with erect, curly, brown hairs; petals brown to chocolate-coloured in vivo, narrowly elliptic to elliptic, 13–27{–32} by 5–15 mm, outer side densely covered with erect, curly, brown hairs; stamens 1–1.5 mm long, connective shield glabrous. *Monocarps* 10–40, green, maturing blue-black in vivo, blackish in sicco, ellipsoid, 10–16 by 7–9 mm, sparsely covered with erect, curly, brown hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall c. 1 mm thick, wrinkled in sicco, stipes 9–15 by 1–2 mm. *Seed* ellipsoid, 10–12 by 5–6 mm, dark brown, smooth to pitted, raphe not distinct from rest of seed.

Distribution — Panama, Colombia (Chocó), Brazil (Roraima).

Habitat & Ecology — In forest, sometimes along roadsides. At elevations of 0–300(–540) m. Flowering: January, February, June, July; fruiting: February, June.

Vernacular name — Panama: Yayo (*Howell 20*).

Notes — *Guatteria aberrans* is remarkable by its pointed flower buds (a feature only sometimes seen in *G. ucayalina* and *G. pannosa*). Another noteworthy aspect in collections from Panama are its chocolate-brown petals. A further peculiarity of this species is that the inner petals seem to stay closed during the whole life cycle (no open bud development seen).

Cogollo & Brand 373 (JAUM, MO) from Colombia, Antioquia, Mun. San Luis, Highway Medellín-Bogotá, 2 km from Río Claro, near Río Samaná, alt. 790 m, probably belongs to this species. It matches *G. aberrans* in almost all aspects (pointed flower buds, leaf size and flower size). Its flowers are annotated as pink ('rosada') and its fruits as black.

Sá et al. 3 (K) from Brazil, Roraima, Rorianópolis, Rio Xixuaú, alt. 36 m is placed here although it is geographically quite far from the localities in Panama and the Pacific coast of Colombia. It shares almost all flower and leaf features, but the branchlets are glabrous or sparsely covered with minute hairs at most, and the pedicels and leaves are covered with appressed instead of erect hairs.

2. *Guatteria acrantha* Erkens & Maas — Map 2

Guatteria acrantha Erkens & Maas in Erkens et al. (2006) 202, t. 1, f. 2, 3. — Type: *Rivera 355* (holo STRI; iso MO, PMA, U), Panama, Los Santos, Distr. Tonosí, Cerro Los Piraguales, El Cortezo, 900 m, 20 April 1994.

Tree or shrub 4–20 m tall; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 1–3 mm long, c. 1 mm diam; lamina narrowly obovate to narrowly elliptic, 5–8 by 2–3.5 cm (leaf index 2.2–2.8), chartaceous, not verruculose, dull, dark brown above, brown to brownish green below, glabrous above, rather densely covered with appressed hairs below, base attenuate, apex rounded or sometimes very shortly and bluntly acuminate (acumen < 2 mm long), primary vein flat to slightly impressed above, secondary veins distinct, 6–9 on either side of primary vein, flat to slightly raised above, smallest distance between loops and margin 1–2 mm, tertiary veins flat to slightly raised above, reticulate. *Flowers* solitary, terminal or also in axils of leaves; flowering and fruiting pedicels 5–12 mm long, c. 1 mm diam, densely covered with appressed, brown hairs, articulated at 0.2–0.3 from the base, bracts of terminal flowers 1–2, foliaceous (?), soon falling, not seen, bracts of axillary flowers c. 5, soon falling, not seen; flower buds broadly ovoid; sepals free, broadly ovate-triangular, 3–5 by 3–4 mm, appressed to reflexed, outer side densely covered with appressed, brown hairs; petals greenish in vivo, broadly ovate-triangular, 7–9 by 5–7 mm, outer side densely covered with appressed, brown hairs; stamens 1–1.5 mm long, connective shield papillate. *Monocarps* c. 10, green in vivo, black in sicco, narrowly ellipsoid, 7–10 by 3–4 mm, subglabrous, apex apiculate (apiculum c. 1 mm long), wall c. 0.1 mm thick, stipes 1–2 by 1 mm. *Seed* narrowly ellipsoid, c. 8 by 3 mm, brown, pitted to rugose and more or less distinctly longitudinally grooved, raphe distinct, flat to slightly raised.

Distribution — Panama (Chiriquí, Los Santos, Veraguas).

Habitat & Ecology — In cloud forest. At elevations of 900–1500 m. Flowering: February to April, July; fruiting: April.

Note — *Guatteria acrantha* is unique by its solitary terminal, minute flowers and by its very tiny, mostly roundish tipped leaves. Superficially, it looks similar to *G. rotundata* by the shape of its leaves, but it is quite distinct by having terminal flowers.

3. *Guatteria aeruginosa* Standl. — Plate 1a, b; Map 2

Guatteria aeruginosa Standl. (1929) 206; R.E.Fr. (1939) 522, f. 35g. — Type: *Cooper 526* (holo F; iso BM, G, K, NY, US), Panama, Bocas del Toro, Region of Almirante, Jan. 1928.

Tree 5–25 m tall, 10–55 cm diam; young twigs densely covered with long-persisting, erect, brown hairs. *Leaves*: petiole 1–8 mm long, 2–4 mm diam; lamina narrowly elliptic or narrowly oblong-elliptic to narrowly obovate, 18–42 by 5–16 cm (leaf index 2.2–4.2), chartaceous, densely verruculose to less often not verruculose, dull, greenish grey, grey, to dark brown above, brown below, sparsely covered with appressed hairs to glabrous above, but primary vein densely covered with erect, brown hairs, densely to sparsely covered with erect, brown hairs below, base acute to obtuse, often slightly decurrent along petiole, apex acuminate (acumen 5–20 mm long), primary vein flat to impressed or rarely raised above, secondary veins distinct, 12–24 on either side of primary vein, flat to raised above, smallest distance between loops and margin 2–5 mm, tertiary veins slightly raised above, reticulate. *Flowers* solitary on leafless branchlets or in axils of leaves; flowering and fruiting pedicels 13–30 mm long, 1–2 mm diam, fruiting pedicels to c. 4 mm diam, densely covered with erect brown hairs, articulated at

Plate 1 a, b. *Guatteria aeruginosa* Standl. a. Flowering branch; b. flower and fruit . – c. *Guatteria alata* Maas & Setten. Part of twig. – d. *Guatteria allenii* R.E.Fr. Flowers. – e–g. *Guatteria alta* R.E.Fr. e. Flowering branch; f. flower; g. fruit. – h. *Guatteria australis* A.St.-Hil. Ripe flower (a: *Chatrou et al. 720*; b: *Chatrou et al. 741*; c: *McPherson 20133*; d: *Maas et al. 9543*; e–g: *Gal Tadri 560*; h: *Maas et al. 8816*). — Photos: a, b: L.W. Chatrou; c: G. Mc Pherson; d: P.J.M. Maas; e–g: Gal Tadri; h. P.J.M. Maas.

0.2–0.6 from the base, bracts 4–7, soon falling, only lowermost bract seen, broadly elliptic, c. 2 mm long; flower buds depressed ovoid to subglobose, slightly pointed or not; sepals free, broadly ovate-triangular, 4–10{–16} by 5–9{–14} mm, appressed, later becoming reflexed, outer side densely covered with appressed and erect, brown hairs; petals yellowish green or creamy yellow in vivo, ovate, ovate-oblong to ovate-trullate, 13–32{–35} by 6–22{–27} mm, outer side densely covered with appressed and erect, brown hairs; stamens 1.5–2.5 mm long, connective shield papillate to hairy. *Monocarps* 20–50, green, maturing purple-black in vivo, black in sicco, ellipsoid, 8–12{–15} by 4–6{–11} mm, glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.2–0.3 mm thick, stipes 5–10 by 1–2 mm. *Seed* ellipsoid, 8–10 by 4–5 mm, brown, rugose, raphe impressed.

Distribution — Honduras, Nicaragua, Costa Rica, Panama, Colombia.

Habitat & Ecology — In forest. At elevations of 0–1200 m, to 1725 m in Colombia. Flowering: throughout the year; fruiting: throughout the year.

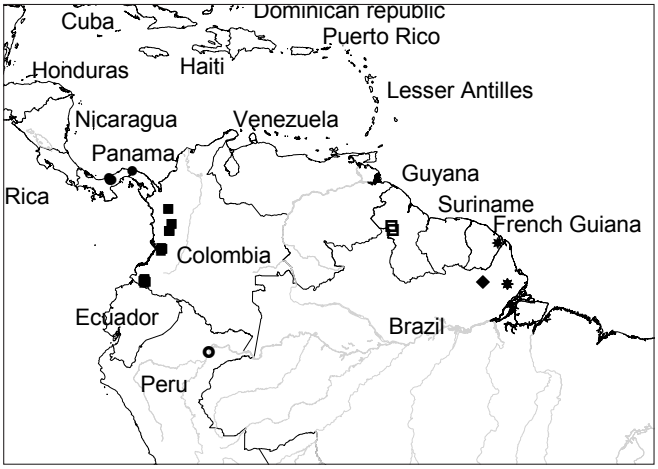
Vernacular names — Honduras: Anona (*Kelly et al. 14/359*), Anona de montaña (*Kelly et al. 23/132*), Sangro blanco (*Kelly et al. 23/132*).

Note — *Guatteria aeruginosa* is characteristic by its dense indument of erect, brown hairs and, in part, by densely verruculose leaves. The basal part of the pedicels is often provided with 2–3 remnants of bracts. There is considerable variation in the density of the tiny warts on leaves. While most specimens collected in Panama have densely verruculose leaves, material from Honduras, Nicaragua, the Heredia region in Costa Rica, the Bocas del Toro region in Panama and Colombia have less densely verruculose or even non-verruculose leaves, but otherwise match *G. aeruginosa* well in all other features.

4. *Guatteria alata* Maas & Setten — Plate 1c; Map 3

Guatteria alata Maas & Setten (1988) 250, f. 8, 9. — Type: *Alverson et al. 1955* (holo WIS 2 sheets; iso CR), Panama, Coclé, Alto Calvario, 0.5–2 km N of Rivera saw mill, on summit and Caribean slope of continental divide, 7 km N by air of El Copé, 700–900 m, 27 Oct. 1982.

Tree 5–30 m tall, c. 20 cm diam; young twigs with sharp wings decurrent from petioles, sparsely to rather densely covered with appressed, brown hairs, soon glabrous. *Leaves*: petiole 10–15 mm long, 5–7 mm diam; lamina obovate to elliptic, 18–34 by 10–16 cm (leaf index 1.9–2.5), coriaceous, rather densely to densely verruculose, dull, brown to green above, brown below, sparsely covered with appressed hairs to glabrous above, sparsely covered with appressed hairs to glabrous below, base acute to obtuse, decurrent as wings along petiole, apex shortly acuminate (acumen 1–5 mm long), primary vein impressed above, secondary veins distinct, 17–20 on either side of primary vein, flat to raised above, smallest distance between loops and margin 1–3 mm, tertiary veins inconspicuous, flat to slightly raised above, reticulate to percurrent. *Flowers* solitary on leafless branchlets; pedicels 12–33 mm long, c. 2 mm diam, fruiting pedicels 3–5 mm diam, densely covered with appressed, pale brown hairs, articulated at c. 0.2 from the base, bracts 7–8, soon falling, not seen; flower buds depressed ovoid; sepals free, broadly ovate, 10–13 by 9–10 mm, appressed, outer side densely covered with appressed, pale brown hairs; petals yellow in vivo, broadly ovate, 13–15 by 10–13 mm, outer side densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 6–20, green to purple in vivo, black in sicco, ellipsoid, 18–24 by 12–15 mm, sparsely covered with appressed, brown hairs, soon glabrous, apex rounded to apiculate (apiculum < 1 mm long), wall 1–2 mm thick, stipes 4–22(–30) by 1–3 mm. *Seed* ellipsoid to ovoid, 15–19 by 7–8 mm, brown, rugulose, raphe not distinct from rest of seed.



Map 3 Distribution of *Guatteria alata* (●), *G. alba* (⭘), *G. alta* (■), *G. alticola* (□), *G. amapaensis* (◆) and *G. anteridifera* (✱).

Distribution — Costa Rica, Panama.

Habitat & Ecology — In forest. At elevations of 200–900 m. Flowering: February, October; fruiting: January, February, October.

Vernacular names — Not recorded.

Field observations — Fruit eaten by the bird *Penelope purpurascens* ('Pava crestada') (*L. Martínez et al.1038*, Panama).

Note — *Guatteria alata* is unique by strongly winged young twigs and broad and obovate to elliptic, shortly acuminate leaves.

5. *Guatteria alba* Maas & Westra, *sp. nov*. — Fig. 10; Map 3

Arbor parva, petalis albis pro genere minimis et petiolis tenellis facile recognoscenda. — Typus: *Rimachi Y. 2714* (holo MO), Peru, Loreto, Maynas, Distr. Iquitos, Carretera de Peña Negra at 25 km from Iquitos, 30 Nov. 1976.

Tree c. 3 m tall, diam not recorded; young twigs turning whitish, rather densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 3–6 mm long, c. 0.5 mm diam; lamina narrowly elliptic to narrowly ovate, 6–9 by 2–3.5 cm (leaf index 2.4–4), chartaceous, not verruculose, dull, dark blackish brown above, brown below, glabrous above or primary vein sparsely covered with appressed hairs, sparsely covered with appressed hairs below, base acute to obtuse, apex acuminate (acumen 5–15 mm long), primary vein flat above, secondary veins distinct, 10–12 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* mostly solitary or sometimes in 2-flowered inflorescences in axils of leaves or often on leafless branchlets; pedicels 13–30 mm long, ≤ 1 mm diam, rather densely covered with appressed hairs, articulated at 0.2–0.4 from the base, bracts 5–7, soon falling, few basal ones seen, broadly ovate, c. 1 mm long, occasionally a foliaceous bract observed (below the articulation), shape as in normal leaves, c. 30–40 by 10–11 mm; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–4 by 3–4 mm, margins and apex reflexed, outer side densely covered with appressed, brown hairs; petals white in vivo, ovate, 6–8 by 2.5–4 mm, outer side densely covered with appressed, brown hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* and *seed* not seen, but fruit mentioned on label as green (*Rimachi Y. 2714*).

Distribution — Amazonian Peru (Loreto).

Habitat & Ecology — In non-inundated forest, on sandy soil. At an elevation of c. 120 m. Flowering: November, December; fruiting: unknown.

Vernacular names — Peru: Anona (*Rimachi Y. 2714*), Espintana (*Rimachi Y. 9860*).

Fig. 10 *Guatteria alba* Maas & Westra. Flowering branch (*Rimachi Y. 2714*; holotype MO).

Other specimens examined. Peru, **Loreto**, Maynas, Distr. Iquitos, Carretera de Zungaro Cocha, margen del terreno de la 'FAP', 120 m, 19 Dec. 1990, *Rimachi Y. 9860* (MO, US).

Notes — *Guatteria alba* is unique in the genus by its very small petals 6–8 mm long that are reported to be white. Other features are the very narrow petioles, and sepals with recurved apex and margins. Two collections are known so far, both from the surroundings of Iquitos and growing on sand. It is somewhat surprising that, given the area of Iquitos having been well-collected, only two gatherings of this species exist.

The white colour of the petals of *G. alba* is unusual in the genus where flowers during their (long) development mostly are green and turn into yellow only in the very short stage of anthesis. Small white flowers are rather reminiscent of, e.g., *Unonopsis* and *Bocageopsis*, and therefore field observations should be interesting.

Guatteria alba differs from another small-flowered species, the Venezuelan *G. stenopetala*, by much smaller pedicels (13–25 vs 30–40 mm long).

6. *Guatteria allenii* R.E.Fr. — Plate 1d; Map 2

Guatteria allenii R.E.Fr. (1950a) 336. — Type: *P.H. Allen 1900* (holo S; iso EAP, F, GH, MO, US), Panama, Coclé, North rim of El Valle de Antón, 9 July 1937.

Tree or rarely a shrub (1–)4–12 m tall, 5–35 cm diam; young twigs densely covered with erect, brown hairs, soon glabrous. *Leaves*: petiole 2–7 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly obovate, 10–21 by 3–8 cm (leaf index 2–3), chartaceous, not verruculose, dull, green to greenish brown above, green below, sparsely covered with appressed and erect hairs to glabrous above, rather densely covered with erect, brown hairs below, base acute, apex acuminate (acumen 5–20 mm long), primary vein flat to slightly raised above, secondary veins distinct, 8–12 on either side of primary vein, slightly raised above, smallest distance between loops and margin 1–2 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; flowering and fruiting pedicels 8–20 mm long, 0.5–1 mm diam, densely covered with appressed brown hairs, articulated at 0.2–0.3 from the base, bracts 4–6, soon falling, one uppermost bract seen, broadly elliptic, 5–7 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 2–5 by 3–5 mm, reflexed, outer side densely covered with appressed, brown hairs; petals yellowish green, maturing canary yellow in vivo, oblong-ovate, 10–15{–25} by 5–9{–15} mm, outer side densely covered with appressed hairs; stamens 1–2 mm long, connective shield hairy. *Monocarps* 25–50, green, maturing dark purple to black in vivo, black in sicco, ellipsoid, 9–11 by 4–5 mm, sparsely covered with appressed hairs, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 4–8 by c. 1 mm. *Seed* ellipsoid, 9–10 by c. 4 mm, dark brown, rugose, raphe impressed.

Distribution — Panama.

Habitat & Ecology — In forest. At elevations of 700–1100 m. Flowering: February, May to July; fruiting: July, September to November.

Vernacular names — Not recorded.

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

7. *Guatteria alta* R.E.Fr. — Fig. 11; Plate 1e–g; Map 3

Guatteria alta R.E.Fr. (1950a) 336, pl. 3. — Type: *Cuatrecasas 14898* (holo S 2 sheets; iso COL 2 sheets, F 2 sheets, S, US), Colombia,Valle del Cauca, Cordillera Occidental, vertiente occidental, mouth of Río Digua, left bank, Piedra de Moler, 900–1180 m, 19 Aug. 1943.

Tree 4–30 m tall, 5–80 cm diam; young twigs zigzagging, rather densely to densely covered with erect, brown hairs, soon glabrous. *Leaves*: petiole 1–4 mm long, 1–1.5 mm diam; lamina narrowly elliptic to narrowly obovate, 12–20 by 3–6 cm (leaf index 3.2–4.2), chartaceous, not verruculose, dull, brown above, pale brown to green below, sparsely covered with appressed to half-appressed, brown hairs to glabrous above, rather densely to densely covered with erect, brown hairs below, base acute, rarely attenuate, apex acuminate (acumen 10–20 mm long), primary vein slightly impressed above, secondary veins distinct, 12–18 on either side of primary vein, slightly impressed above, smallest distance between loops and margin 2–4 mm, tertiary veins slightly impressed above, reticulate. *Flowers* solitary in axils of leaves; pedicels 35–60 mm long, 1–1.5 mm diam, fruiting pedicels to c. 2.5 mm diam, rather densely to sparsely covered with erect, brown hairs, articulated at 0.2–0.4 from the base, bracts 4–6, soon falling, basal one c. 1 mm long, no other bracts seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–7 by 5–7 mm, appressed, outer side sparsely covered with appressed, brown hairs; petals pale green, green, or yellow in vivo, ovate to broadly ovate, 8–15 by 7–10 mm, outer side densely covered with appressed, brown hairs; stamens c. 2 mm long, connective shield hairy. *Monocarps* 20–30, green to dark green, maturing black in vivo, blackish in sicco, ellipsoid to obovoid, rarely narrowly ellipsoid, 7–10 by 4–6 mm, sparsely covered with appressed, brown hairs, soon glabrous, apex apiculate (apiculum 0.2–0.6 mm long), wall 0.1–0.2 mm thick, stipes 5–9 by 0.5–1 mm. *Seed* ellipsoid, 7–9 by 4–5 mm, dull, reddish brown to pale brown, rugose, raphe impressed.

Distribution — Pacific coast of Colombia (Antioquia, Chocó, Nariño, Valle del Cauca).

Habitat & Ecology — In wet, premontane, primary or secondary forest, on steep slopes and along river margins. At elevations of 250–1700 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular name — Colombia: Guasca negra (*Betancur et al. 4312*).

Notes — *Guatteria alta* can be recognized by a combination of a dense indument of erect, brown hairs on young twigs and lower side of the leaves, chartaceous, non-verruculose, narrowly elliptic to narrowly obovate, shortly petiolate leaves, and pedicels up to 60 mm long.

Betancur et al. 4312 (MO) from the Municipality of Barbacoas, Nariño, Colombia is aberrant by larger and narrowly ellipsoid monocarps (c. 17 by 6 mm) and larger seeds (c. 14 by 6 mm).

In *Pipoly et al. 18048* (U) some growth apices have aborted, the axillary inflorescence immediately below seemingly becoming terminal, with or without foliaceous, elliptic bracts to c. 40 by 17 mm.

8. *Guatteria alticola* Scharf & Maas — Map 3

Guatteria alticola Scharf & Maas in Scharf et al. (2005) 565, f. 1. — Type: *Clarke et al. 9247* (holo U; iso BRG), Guyana, Mt Ayanganna, East face, base of escarpment, 1120 m, 16 June 2001.

Tree 3–6 m tall, diam not recorded; young twigs densely covered with erect hairs to c. 1.5 mm long, finally glabrous. *Leaves*: petiole 2–4 mm long, 1–2 mm diam; lamina narrowly elliptic, 10–15 by 3–5.5 cm (leaf index 2.8–3.3), chartaceous, not verruculose, dull, pale to dark brown above, yellowish brown below, rather densely to sparsely covered with erect hairs to glabrous above and below, base acute to attenuate, apex acuminate (acumen 5–20 mm long), primary vein slightly raised above, secondary veins distinct, 6–10 on either side of primary vein, slightly raised above, smallest distance between loops and margin 2–3 mm, tertiary veins flat above, reticulate. *Flowers*

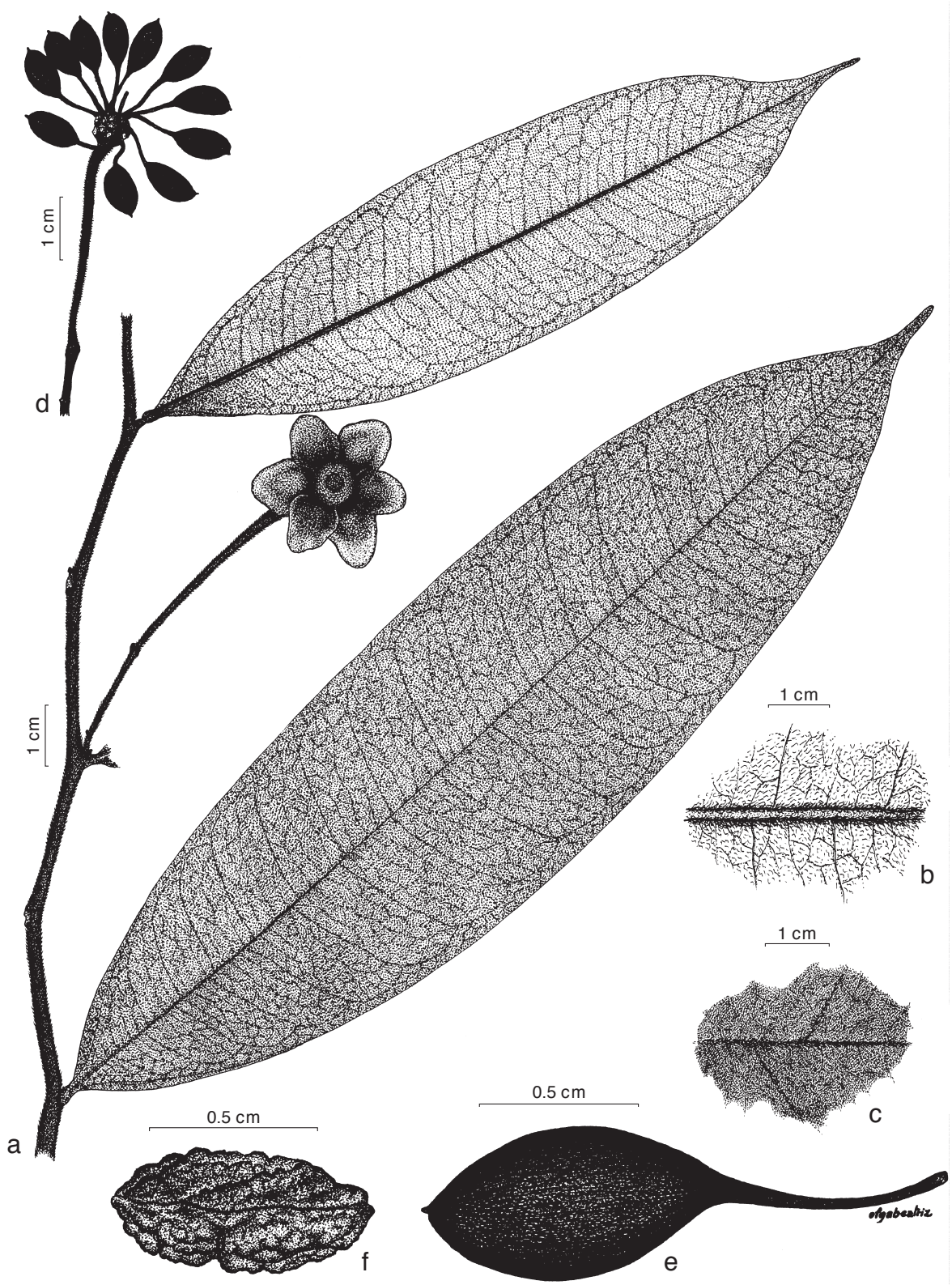


Fig. 11 *Guatteria alta* R.E.Fr. a. Flowering branch; b. lower side of lamina; c. upper side of lamina; d. fruit; e. monocarp; f. seed (a–d, f: *Devia A. 609*; e: *Cuatrecasas 14898*; isotype COL; from Sánchez S. (1986) f. 15.

solitary in axils of leaves; pedicels 25–30(–35) mm long, 1–1.5 mm diam, rather densely covered with erect hairs, articulated at 0.3–0.4 from the base, bracts c. 5, soon falling, not seen; flower buds subglobose; sepals free, broadly ovate-triangular, c. 4 by 3–4 mm, appressed, outer side densely covered with erect hairs; petals green in vivo, oblong-elliptic, 15–18 by 7–8 mm, outer side densely covered with erect, curly hairs; stamens c. 2 mm long, connective shield papillate, umbonate. *Monocarps* and *seed* not seen, but mentioned on the label: 'fruit green with red stipes'.

Distribution — Guyana.

Habitat & Ecology — In dense forest, on sandstone and peat and riparian vegetation near waterfall, with *Protium*, *Socratea* and *Clusia*. At elevations of 1120–1650 m. Flowering: June, December; fruiting: June.

Vernacular names — Not recorded.

Note — *Guatteria alticola* looks superficially like another Guianan endemic, *G. wokomungensi*s, but it differs from that species in having long-persistent, erect hairs on the young twigs instead of having glabrous young twigs.

Fig. 12 *Guatteria amapaensis* Maas & Westra. Flowering branch (*Rabelo 3132*; isotype K).

9. *Guatteria amapaensis* Maas & Westra, *sp. nov.* — Fig. 12, 13a; Map 3

Species praecipue monocarpiis dense lanatis et seminibus rugosis bene distincta. — Typus: *Rabelo et al. 3132* (holo U; iso K, MO, NY), Brazil, Amapá, Mun. Macapá, 13 km SE of Riozinho on highway 'Perimetral Norte' (BR 210), 1 Jan. 1985.

Tree 4–12 m tall, c.16 cm diam; young twigs densely covered with erect hairs, soon glabrous. *Leaves*: petiole 10–15 mm long, 1–2 mm diam; lamina narrowly elliptic, 15–26 by 4.5–9 cm (leaf index 2.9–3.9), chartaceous, not verruculose, dull, dark brown above, brown below, glabrous above, rather densely covered with erect hairs below, base long-attenuate, apex acuminate (acumen 10–20 mm long), primary vein impressed above, secondary veins distinct, c. 15 on either side of primary vein, impressed above, smallest distance between loops and margin 2–3 mm, tertiary veins flat to slightly raised above, percurrent. *Flowers* in 1–2-flowered inflorescences, in axils of leaves or (fruiting) on leafless branchlets; flowering and fruiting pedicels 5–10 mm long, c. 2 mm diam, densely covered with erect and appressed, woolly hairs, articulated at 0.2–0.4 from the base, bracts 4–5, soon falling, the basal ones to c. 2 mm long, the 2 upper ones ovate-traingular, c. 4 mm long; flower buds conical, pointed; sepals free, broadly ovate-triangular, 3–6 by 4–5 mm with markedly acuminate apex, appressed, outer side densely covered with erect and appressed, wooly hairs; petals greenish in vivo, narrowly ovate-triangular, 11–13 by 4–5 mm, outer side densely covered with erect and appressed, wooly hairs; stamens c. 2 mm long, connective shield densely hairy. *Monocarps* c. 20, red in vivo, greyish brown in sicco, ellipsoid, 13–15 by 7–9 mm, densely covered with erect hairs, apex rounded, wall c. 0.5 mm thick, stipes 5–11 by 2 mm. *Seed* ellipsoid, 7–12 by 6–7 mm, brown, rugose, raphe not distinct from rest of seed.

Distribution — Brazil (Amapá).

Habitat & Ecology — In non-inundated, moist forest, on steep slope. At about sea level. Flowering: January; fruiting: January.

Vernacular names — Not recorded.

Other specimens examined. Brazil, **Amapá**, Mun. Macapá, Perimetral Norte, 122 km NW of Porto Grande, 1 Jan. 1985, *Daly et al. 4028* (NY, U).

Note — *Guatteria amapaensis*, only known from the type locality, has previously been considered to be an extreme form of *G. blepharophylla* by Maas & Westra (2011) and was included in that species. It is different from it, however, by the total lack of verruculae on the leaves and by the densely hairy monocarps, and also by the rugose seeds.

10. *Guatteria amplifolia* Triana & Planch. — Map 4

Guatteria amplifolia Triana & Planch. (1862) 35; R.E.Fr. (1939) 376. — Type: *Fendler 3* (holo K), Panama, Colón, Chagres, Isthmus of Panama, Feb. 1850.

Guatteria diospyroides Baill. [subsp. *diospyroides*] (1868b) 269; R.E.Fr. (1939) 376. — Type: *Liebman 12* (lecto C, selected by Fries 1939; iso K, P), Mexico, Oaxaca, Chimantla.

Guatteria jurgensenii Hemsl. (1878) 1; R.E.Fr. (1939) 373. — Type: *Jurgensen 718* (holo K; iso B, G), Mexico, Oaxaca, Sierra San Pedro Nolasco, Talea, etc., 1843–1844.

Guatteria diospyroides Baill. subsp. *hondurensis* R.E.Fr. (1939) 378, f. 12b. — Type: *Chickering 189* (holo S; iso F), Honduras, Lancetilla ('Lacertilla'), June–July 1929.

Guatteria inuncta R.E.Fr. [var. *inuncta*] (1939) 378, f. 11a. — Type: *Standley 37132* (holo US 2 sheets; iso F), Costa Rica, Limón, vicinity of Guápiles, 300–500 m, Mar. 1924.

Guatteria inuncta R.E.Fr. var. *minor* R.E.Fr. (1939) 380. — Type: *Brenes 20385* (holo F; iso MO), Costa Rica, Alajuela, Alto de Acosta, NE of San Ramón, 16 Feb. 1935.

Guatteria platypetala R.E.Fr. (1939) 381, f. 11b, c, 12c. — Type: *Deam 50* (holo F; iso US), Guatemala, Puerto Barrios, 26 Feb. 1905.

Guatteria inuncta R.E.Fr. var. *caudata* R.E.Fr. (1955b) 152. — Type: *Von Wedel 2108* (holo MO; iso GH), Panama, Bocas del Toro, Old Bank Island, vicinity of Chiriquí Lagoon, 0–120 m, 17 Feb. 1941.

Tree or shrub 2–12(–20) m tall, 5–30 cm diam; young twigs sparsely to rather densely covered with appressed hairs or glabrous. *Leaves*: petiole 4–13 mm long, 1–7 mm diam; lamina narrowly ovate to narrowly obovate, sometimes ovate or elliptic, 13–40 by 4–15 cm (leaf index 2.6–3.3), chartaceous, not verruculose, dull, greyish brown to grey, brown below, glabrous above, sparsely covered with appressed hairs to glabrous below, base obtuse, cordate (with basal margins revolute), to acute, apex acuminate (acumen 5–30 mm long), primary vein impressed above, secondary veins distinct, 12–20 on either side of primary vein, impressed to flat above, smallest distance between loops and margin 2–4 mm, tertiary veins slightly raised above, reticulate. *Flowers* 1–2(–several)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–15 mm long, c. 1 mm diam, fruiting pedicels 15–40(–55) mm long, 1–2 mm diam, rather densely to sparsely covered with appressed hairs, articulated at 0.2–0.3 from the base, bracts 5–7, soon falling, basal one elliptic to broadly elliptic, 1–1.5 mm long, uppermost similar, c. 1.5 mm long; flower buds depressed ovoid; sepals free or basally connate (*McPherson 7485*), broadly ovate-triangular, 3–12 by 4–10 mm, reflexed to appressed, outer side rather densely to densely covered with appressed hairs; petals green, maturing yellow in vivo, oblong-ovate to oblong-obovate, 10–25 by 5–15 mm, outer side densely covered with appressed hairs; stamens 1–2 mm long, connective shield papillate. *Monocarps* (25–)50–75, green, maturing red to finally black in vivo, black in sicco, ellipsoid, 7–10 by 3–6 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 1 mm long), wall 0.1–0.2 mm thick, stipes 5–25 by 1 mm. *Seed* ellipsoid, 7–10 by 4–6 mm, dark brown, pitted, raphe raised.

Distribution — Mexico (Chiapas, Oaxaca, Tabasco, Veracruz), Guatemala, Honduras, Belize, Nicaragua, Costa Rica, Panama.

Habitat & Ecology — In lowland rain forest or lower montane forest. At elevations of 0–1100(–1850) m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Costa Rica: Malagueto (*Thomson 24*, *447*), Malagueto negro (*Thomson 447*). Honduras: Agua catillo (*Saunders 1192*). Mexico: Equepetz (Zoque language, *Hernández G. & Gonzalez L. 1717*). Panama: Daner (Kuna language, *DeNevers et al. 6423*).

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

Typical *G. amplifolia* is encountered throughout Panama and is characterized by very large leaves and petioles with the second-

Map 4 Distribution of *Guatteria amplifolia*.

Fig. 13 a. *Guatteria amapaensis* Maas & Westra. Fruit. – b. *Guatteria antioquensis* Maas & Westra. Fruit. – c. *Guatteria atabapensis* Aristeg. ex D.M.Johnson & N.A.Murray. Fruiting branch, detail. – d. *Guatteria auyantepuiensis* Maas & Westra. Detail of flower. – e, f. *Guatteria beckii* Maas & Westra. e. Flower; f. fruit. – g. *Guatteria beniensis* Maas & Westra. Young fruit, also note densely erect hairy juvenile parts in upper left. – h. *Guatteria blainii* (Griseb.) Urb. Detail of flower (a: *Daly et al. 4028*, U; b: *E. Correa et al. 93*, U; c: *Wurdack & Adderley 42759*, isotype US; d: *F. Cardona 2619*, holotype US; e, f: *Beck & Haase 9895*, holotype U; g: *Nee 34593*, holotype NY; h: *Ekman 5920*, S).

ary veins distinctly impressed on the upper side; furthermore the leaf base is obtuse to cordate with the basal margins somewhat revolute. Towards the West, in Costa Rica, Nicaragua, and all other western Central American countries, leaves and petioles tend to be smaller, and the secondary veins are less impressed to even flat on the upper side. Moreover, the leaf base is mostly acute, although obtuse leaf bases are also sometimes found. We consider all of the variation to be encompassed within a single species. For an illustration of this variation, see Erkens 2007: 104, f. 1. However, it is clear that this complex should be analysed further morphologically as well as with molecular data.

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

11. *Guatteria anteridifera* Scharf & Maas — Map 3

Guatteria anteridifera Scharf & Maas in Scharf et al. (2008) 517, f. 1–3. — Type: *Sabatier & Prévost 5047* (holo U 2 sheets; iso CAY), French Guiana, km 122.5 of road from Cayenne to Saint Georges, near 'Savane Roche Virginie', 27 July 2006.

Tree up to c. 40 m tall, 50–80 cm diam, with buttresses up to c. 2 m high and c. 80 cm at the base, limbs decurrent; young twigs densely covered with appressed, silvery hairs, soon glabrous. *Leaves*: petiole 15–20 mm long, 2–3 mm diam, winged; lamina obovate to narrowly oblong-elliptic, 9–21 by 5–8 cm (leaf index 1.8–2.7), coriaceous, scabridulous, dull, greyish to greenish brown above, dark brown below, glabrous above, sparsely covered with appressed hairs below, base long-attenuate, apex shortly acuminate (acumen 3–10 mm long), primary vein impressed above, secondary veins distinct, 12–16 on either side of primary vein, slightly impressed above, smallest distance between loops and margin 2–3 mm, tertiary veins inconspicuous, flat above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; flowering and fruiting pedicels 10–15 mm long, 1–2 mm diam, densely to rather densely covered with appressed, silvery hairs, articulated at 0.2–0.3 from the base, bracts 5–6, soon falling, broadly to very broadly ovate at the base, 1–2 mm long, other bracts not seen; flower buds not seen; sepals free, broadly ovate-triangular, 5–6 by 5–6 mm, reflexed, outer side densely covered with appressed, silvery hairs; petals yellowish green in vivo, elliptic, oblong-elliptic, to obovate, 21–23 by 10–13 mm, outer side densely covered with appressed, short, silvery hairs; stamens c. 1 mm long, connective shield hairy, umbonate. *Monocarps* c. 4, green in vivo (immature ones), greyish to blackish brown in sicco, ellipsoid, 20–25 by 8–11 mm, apex sparsely covered with appressed hairs, apex apiculate (apiculum 1–1.5 mm long), wall c. 1 mm thick, stipes 5–8 by 1–1.5 mm. *Seed* ellipsoid, 16–19 by 7–9 mm, pale to dark brown, rugulose to transversely grooved, raphe impressed.

Distribution — French Guiana, Amazonian Brazil (Amapá).

Habitat & Ecology — In non-inundated, primary forest. At about sea level. Flowering: July, August; fruiting: November.

Vernacular names — Not recorded.

Note — *Guatteria anteridifera* is well marked by large buttresses of up to 2 m high. It seems similar to some species of sect. *Mecocarpus* (e.g., *G. blepharophylla*), but it completely lacks the verruculose structures so typical for that section. Instead, it has scabridulous leaves which are covered with minute, circular structures. It perhaps comes closest to the Guyanan endemic *G. paludosa*, but that species lacks the buttresses, has much larger leaves (30–55 cm vs 9–21 cm long in *G. anteridifera*), long-acuminate vs shortly acuminate leaves (acumen 10–45 mm vs 3–10 mm long in *G. anteridifera*) and larger stamens (2–3 mm vs 1 mm long in *G. anteridifera*).

12. *Guatteria antioquensis* Maas & Westra, *sp. nov.* — Fig. 13b, 14; Map 5

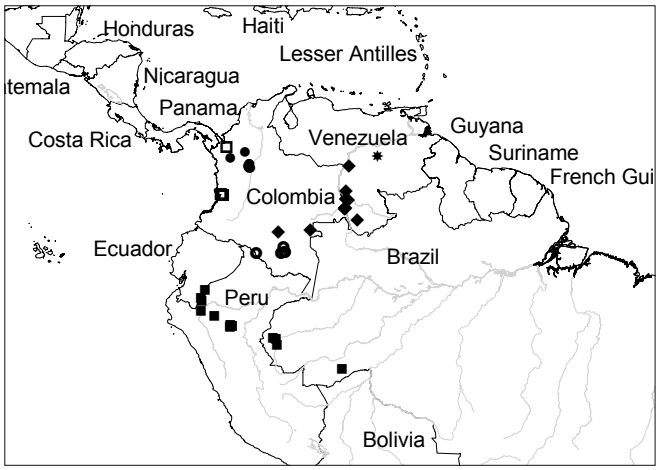
Guatteria citriodora affinis, sed pedicellis longioribus seminibus foveatis bene differt. — Typus: *Cogollo et al. 3796* (holo JAUM 2 sheets; iso COL, MO), Colombia, Antioquia, Mun. San Luis, near Aquitania, 8 km from Hwy. Medellín-Bogotá, 830 m, 25 Nov. 1988.

Tree 5–23 m tall, c. 6 cm diam (once recorded); young twigs densely covered with erect, brown long-persisting hairs. *Leaves*: petiole 3–6 mm long, c. 1 mm diam; lamina narrowly ovate to narrowly elliptic, 10–19 by 3–5 cm (leaf index 2.4–3.6), chartaceous, not verruculose, shiny, dark brown to greyish black above, brown below, sparsely covered with erect hairs mainly along primary vein above, soon glabrous, densely covered with erect, brown hairs, hairs simple or in bundles of 2–4, below, base acute to obtuse, basal margins often revolute, apex acuminate (acumen 5–10 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 1–2 mm, tertiary veins slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences, in axils of leaves; pedicels 15–20 mm long, c. 1 mm diam, fruiting pedicels 20–35 mm long, 1–2 mm diam, densely covered with erect, brown hairs, articulated at 0.2–0.5 from the base, bracts 5–7, soon falling, not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–6 by 3–6 mm, apex and margins often reflexed, outer side densely covered with erect, brown hairs; petals green in vivo, narrowly elliptic to narrowly obovate, 8–20 by 4–9 mm, outer side densely covered with erect to appressed, brown hairs; stamens c. 1.5 mm long, connective shield densely hairy (hairs c. 1 mm long). *Monocarps* c. 50, green, maturing purple-black to red in vivo, black in sicco, ellipsoid to narrowly ellipsoid, 7–10 by 3–4 mm, rather densely to sparsely covered with erect to appressed, brown hairs, to glabrous, apex apiculate (apiculum c. 1 mm long) to rounded, wall c. 0.1 mm thick, stipes 5–10 by 0.5 mm, rather densely to sparsely covered with erect to appressed, brown hairs to glabrous. *Seed* ellipsoid, 7–8 by 4 mm, brown, deeply pitted, raphe raised.

Distribution — Colombia (Antioquia).

Habitat & Ecology — In non-inundated forest. At elevations of 790–1550 m. Flowering: November to February; fruiting: February, June, November, December.

Vernacular names — Colombia: Frisolo (*Cárdenas L. & Ramírez 2746*), Garrapato (*Fonnegra et al. 3109*), Garrapato lanudo (*Giraldo 190*).



Map 5 Distribution of *Guatteria antioquensis* (●), *G. araracuarae* (⭘), *G. arenicola* (■), *G. argentea* (□), *G. atabapensis* (◆) and *G. bernardii* (✷).

Fig. 14 *Guatteria antioquensis* Maas & Westra. Flowering branch (*Cogollo & Estrada 202*; MO).

Other specimens examined. Colombia, **Antioquia**, Mun. San Luis, margen derecha de la carretera Quebradas-Naranjales y la Cristalina, 420–460 m, *Callejas et al. 4151* (HUA); Mun. Amalfí, Veredas Chorritos, La María, Montebello, km 15–35 of the road from Chorritos to Los Monos, SNE of Amalfí, 1180–1550 m, *Callejas et al. 9022* (HUA, NY, U); Mun. San Luis, Vereda La Josefina, Quebrada la Mariola, 700–925 m, *Cárdenas L. & Ramírez 2746* (JAUM); Mun. San Luis, sector Río Samaná-Río Claro, near Vereda Tulipán, 935 m, *Cogollo & Estrada 202* (MO); Mun. San Luis, sector Río Samaná-Río Claro, near Vereda La Josefina, 790 m, *Cogollo & Estrada 299* (MO); Mun. San Luis, El Reposo, km 152 of Hwy. Medellin-Bogotá, sector Río Samaná-Río Claro, 790 m, *Cogollo & Brand 427* (JAUM, MO); Mun. San Luis, near Aquitania, 8 km from Hwy. Medellín-Bogotá, 830 m, *Cogollo et al. 3796* (COL, JAUM, MO); Mun. San Carlos, Vereda Patio Bonito, Alto El Cerrón, linea de transmisión San Carlos-San Marcos (entre las torres 22–23), 1100 m, *E. Correa et al. 93* (U); Mun. San Carlos, road of Vereda Miraflores to the Corregimiento Alto de Samaná Norte, 800–900 m, *Fonnegra et al. 3109* (HUA, MO, U); Mun. Cáceres, Vereda Madreseca, Reserva Regional Natural Bajo Cauca-Nechí, 830–850 m, *Giraldo 190* (JAUM); Mun. San Luis, Vereda La Josefina, Hwy. Medellin-Bogotá, 800 m, *Hoyos M. & Hernández 261* (JAUM, MO); Mun. San Rafael, Vereda El Charco, 1010–1200 m, *Montes Guarín 200* (COL).

Notes — *Guatteria antioquensis*, restricted to the Colombian department of Antioquia, is easily recognizable by a combination of its dense and long-persisting indument of erect hairs (hairs simple or in bundles of 2–4) on the lower side of the leaves and a densely hairy connective shield, which is so typical for all species related to *G. schomburgkiana*. Another peculiarity is the hairy stipes, which in almost all other species in the genus are devoid of any indument.

Guatteria antioquensis looks somewhat like *G. citriodora* because of its indument, but from that species it clearly differs by much longer pedicels, both flowering and fruiting (15–35 vs 5–17 mm), a much higher number of monocarps (c. 50 vs 2–10), a thinner fruit wall (0.1 vs 0.5 mm thick) and pitted instead of smooth seeds.

13. *Guatteria araracuarae* Maas & Westra, *sp. nov.* — Map 5

Guatteria hispida affinis sed foliis vena marginali bene distincta (nec non venis secundariis arcte tantum conjunctis differt. — Typus: *Ronderos & Rosselli 58* (holo COAH), Colombia, Amazonas, cuenca del medio Caquetá, región de Araracuara, Comunidad de Peña Roja, bosque maduro de las terrazas altas del Río Caquetá, 160 m, 17 July 1996.

Guatteria sp. B Murillo A. & Restrepo (2000) 119, f. 36; Maas & Westra (2011) 141, f. 23.

Tree 3.5–16 m tall, 2.5–7 cm diam; young twigs densely to rather densely covered with long-persistent, erect, stiff hairs to c. 3 mm long. *Leaves*: petiole 3–5 mm long, 2–4 mm diam; lamina narrowly elliptic to narrowly obovate, 15–28 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, stiff hairs to c. 3 mm long below, base obtuse, apex 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, at a smallest distance of 2–4 mm from the margin, tertiary veins inconspicuous and hardly visible above, percurrent to reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; flowering and fruiting pedicels (3–)11 mm long, 1–2 mm diam, densely covered with long-persistent, erect, stiff hairs to c. 3 mm long, articulated at c. 0.1 from the base, bracts not countable in available material, uppermost bract ovate-elliptic, to c. 11 mm long; flower buds ovoid; sepals free, broadly ovate-triangular, 8–10 by 5–8 mm, appressed, apex acuminate, outer side densely covered with erect, brown hairs; petals green or white in vivo, oblong-ovate to elliptic, 8–15 by 4–10 mm, outer side densely covered with appressed, wooly hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 5–10, purplish black in vivo, black in sicco, ellipsoid, 15–20 by 8–9 mm, densely to sparsely covered with erect, stiff hairs to c. 2 mm long, apex rounded to apiculate (apicule < 1 mm long), wall 0.5–0.7 mm thick, stipes 10–20 by 1 mm, densely covered with erect hairs. *Seed* ellipsoid, c. 15 by 7 mm, dark brown, horizontally and transversely grooved, raphe not distinct from rest of seed.

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, July.

Vernacular names — Colombia: Buruchicu (Muinane name) (*Van Andel et al. 160*), Carguero (Muinane name) (*Cárdenas L. et al. 4064*), Dujïku (Huitoto name) (*Cárdenas L. et al. 4064*), Jïdïra (Huitoto name) (*Cárdenas L. et al. 4064*), Ñaajeku (Muinane name) (*Murillo A. et al. 510*).

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

Notes — *Guatteria araracuarae* looks similar to *G. hispida* as to the leaf shape and the dense indument of stiff erect hairs. It clearly differs from the latter, however, by the presence of a distinct marginal leaf vein, while in *G. hispida* the leaves do not show a marginal vein.

Murillo A. & Restrepo (2000) attributed the collection *Stein et al. 4002* (MO, U) from Loreto, Peru, to this species as well. Actually, it is the type collection of *G. grandipes* Maas & Westra (2011).

14. *Guatteria arenicola* Maas & Erkens — Plate 2a, b; Map 5

Guatteria arenicola Maas & Erkens in Erkens et al. (2008) 471, f. 1, pl. 1. — Type: *Maas et al. 8980* (holo U; iso NY), Brazil, Acre, km 6 of road from Cruzeiro do Sul to Boa Fé (BR-307), Ramal dos Carobas, c. 200 m, 16 Oct. 2001.

Shrub or tree 2–30 m tall, 5–40 cm diam, trunk fissured, slash orange (in material from Acre); young twigs densely to sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2–7 mm long, c. 1 mm diam; lamina elliptic to narrowly elliptic, 5–9 by 1–3 cm (leaf index 2–3.6), coriaceous to chartaceous, not verruculose, dull, dark brown, brownish black to greyish black above, somewhat paler brown below, glabrous, except for the hairy primary vein above, rather densely to sparsely covered with appressed hairs below, base attenuate to acute, apex shortly and bluntly acuminate (acumen 1–3 mm long) to rounded, primary vein slightly impressed to flat above, secondary veins indistinct to distinct, 6–13 on either side of primary vein, flat to raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels strongly recurved (in material from Acre) to erect, 10–13 mm long, c. 1 mm diam, fruiting pedicels 15–20 mm long, c. 2 mm diam, articulated at 0.2–0.5 from the base, bracts 4–5, the 2 upper ones narrowly obovate, 4–6 by 1.5–2 mm, the 3 lower ones 1–1.5 mm long, densely to sparsely covered with appressed hairs; flower buds depressed ovoid, slightly pointed; sepals free or basally connate, broadly ovate-triangular, 3–6 by 3–5 mm, initially appressed, soon spreading and apically reflexed, outer side densely to rather densely covered with appressed hairs; petals green, maturing yellow in vivo, ovate, 5–18 by 3–12 mm, outer side densely covered with appressed to erect hairs; stamens 1–1.5 mm long, connective shield papillate to hairy. *Monocarps* 10–40, green, maturing black in vivo, brownish black in sicco, ellipsoid, 7–13 by 3–7 mm, sparsely covered with appressed hairs, soon glabrous,

Plate 2 a, b. *Guatteria arenicola* Maas & Erkens. a. Fruiting branches; b. fruits. – c. *Guatteria beckii* Maas & Westra. Fruiting branch. – d. *Guatteria argentea* Erkens & Maas. Top of branchlet showing silvery indument; e. fruits. – f, g. *Guatteria blainii* (Griseb.) Urb. f. Flower; g. fruit (a, b: *Rodriguez R.3095*; c: *Solomon 16789*; d, e: *Maas et al. 10525*; f, g: *Maas & Mejia 6443*). — Photos: a, b: E. Rodriguez R.; c: J. Solomon; d–g: P.J.M. Maas.

apex rounded to bluntly apiculate (apiculum < 0.5 mm long), wall 0.3–0.5 mm thick, stipes 0–2 by 1.5–2 mm. *Seed* ellipsoid, 10–11 by 3–5 mm, pale brown, smooth, raphe not distinct from rest of seed.

Distribution — Amazonian Ecuador (Zamora-Chinchipe), Peru (Cajamarca, San Martín), Brazil (Acre).

Habitat & Ecology — In campina or campinarana vegetation, or in primary forest, on white, often humous sand. At elevations of 200–2170 m. Flowering: June, September to November; fruiting: May, December.

Vernacular names — Not recorded.

Notes — *Guatteria arenicola* is a small-leaved species from the white sand campina or campinarana vegetations of Acre, Brazil, and forests on white sands in Peru (San Martín). It is quite noteworthy by its tiny, prominently veined, coriaceous leaves, its very small flowers, which often have strongly recurved pedicels, and strongly rugose seeds. Another character of this species is the presence of orange slash, a feature not seen so far in any other representative of the genus *Guatteria*.

Guatteria arenicola has been compared with *G. rupestris*, a species which is known from the cerrados in Minas Gerais, Brazil. They both share some leaf characteristics, but in *G. rupestris*, the leaves mostly have a rounded to even emarginate apex, whereas the basal margins are revolute.

15. *Guatteria argentea* Erkens & Maas — Plate 2d; Map 5

Guatteria argentea Erkens & Maas in Erkens et al. (2008) 473, f. 2. — Type: *Monsalve B.1262* (holo U; iso CUVC, MO), Colombia, Valle del Cauca, Bajo Calima, Concesión Pulpapel/Buenaventura, 100 m, 13 Nov. 1986.

Tree 6–12 m tall, diam not recorded; young twigs densely covered with appressed, silvery hairs, soon glabrous. *Leaves*: petiole 8–15 mm long, 2–3 mm diam; lamina obovate, rarely narrowly so, 9–12 by 3.5–6 cm (leaf index 2–2.5), coriaceous, densely verruculose, slightly shiny, dark brown to greyish black above, brown below, glabrous above, densely covered with appressed, silvery hairs below, base attenuate, apex shortly acuminate (acumen 1–5 mm long), primary vein impressed above, keeled below, secondary veins distinct, 9–13 on either side of primary vein, raised to flat above, smallest distance between loops and margin 3–4 mm, tertiary veins slightly raised to flat above, reticulate. *Flowers* solitary in axils of leaves; pedicels 5–9 mm long, 1–2 mm diam, fruiting pedicels 10–15 mm long, c. 2 mm diam, densely to rather densely covered with appressed, silvery hairs, articulated at 0.3–0.5 from the base, bracts 3–4, soon falling, the upper one c. 4 by 3 mm; flower buds depressed ovoid to ovoid; sepals free, broadly ovate-triangular, 3–5 by 4–6 mm, appressed, outer side densely covered with appressed, silvery hairs; petals yellowish green in vivo, elliptic to obovate, 9–13 by 5–8 mm, outer side densely covered with appressed, silvery hairs; stamens 1–1.5 mm long, connective shield hairy. *Monocarps* 10–15, green to yellow in vivo, brown to blackish in sicco, ellipsoid, 12–16 by 5–8 mm, sparsely covered with appressed hairs, apex apiculate (apiculum < 0.5 mm long), wall 1–1.5 mm thick, stipes 2–6 by c. 2 mm. *Seed* ellipsoid, 10–12 by c. 5 mm, shiny, dark brown, pitted, raphe not distinct from rest of seed.

Distribution — Colombia (Antioquia, Valle del Cauca).

Habitat & Ecology — In forest ('bosque pluvial tropical'). At elevations of 50–200 m. Flowering: February, August, October to December; fruiting: February, August, November, December.

Vernacular names — Not recorded.

Notes — *Guatteria argentea* is very easily recognizable by its silvery indument on many parts of the plant and by its obovate, densely verruculose leaves with an attenuate base.

The type of the present species (*Monsalve B.1262*) has been used by Erkens et al. (2007a, b) for a phylogenetic study on *Guatteria*. However, in these studies this specimen was assigned to *G. heterotricha* R.E.Fr. It was placed sister to *G. rotundata* to which it looks quite similar. *Guatteria rotundata* is from Panama (Panamá and San Blas) and the two species share the obovate leaves. *Guatteria argentea* differs by its dense silvery indument of the young twigs and lower side of the lamina and by its more densely verruculose leaves.

16. *Guatteria atabapensis* Aristeg. ex D.M.Johnson & N.A. Murray — Fig. 13c, 15; Map 5

Guatteria atabapensis Aristeg. ex D.M.Johnson & N.A.Murray (1990) 599; Steyerm. et al. (1995) 444; Murillo A. & Restrepo (2000) 92. — Type: *Wurdack & Adderley 42759* (holo NY; iso F, G, RB, US, VEN), Venezuela, Amazonas, Dep. Atabapo, Río Atabapo, margin of Sabana Cumare, right bank of Caño Cumare (20 km above San Fernando de Atabapo), 125–140 m, 3 June 1959.

Tree or shrub, 3–6(–28) m tall, to 23 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 5–10 mm long, 1–3 mm diam; lamina elliptic to ovate or narrowly so, 8–16 by 4–6 cm (leaf index 1.8–2.8), coriaceous, not or less frequently verruculose, dark brown to greyish green above, brown to pale brown below, glabrous above, sparsely covered with appressed hairs to almost glabrous below, base obtuse, sometimes acute, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins indistinct, 10–14 on either side of primary vein, raised above, smallest distance between loops and margin 4–7 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; flowering and fruiting pedicels 4–8 mm long, 1–2 mm diam, rather densely covered with appressed hairs, articulated at c. 0.3 from the base, bracts 4–6, soon falling, broadly ovate, 1–3 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–5 by 4–5 mm, spreading, outer side densely covered with appressed hairs; petals greenish yellow or yellow in vivo, ovate to obovate, 8–23 by 4–12 mm, outer side densely to rather densely covered with appressed hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* 10–25, green, maturing black in vivo, black to brownish in sicco, ellipsoid, 7–10 by 4–6 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum 0.1–0.2 mm long), wall 0.2–0.3 mm thick, stipes 1–5 by 1 mm. *Seed* ellipsoid-fusiform, 7–9 by 4–5 mm, dark brown, pitted to transversely grooved, raphe impressed.

Distribution — Amazonian Colombia (Vaupés), Venezuela (Amazonas, Bolívar).

Habitat & Ecology — In shrub islands in savannas and in forest, on white sands. At elevations of 0–150(–560) m. Flowering: January to May; fruiting: January, May, July, September.

Vernacular names — Colombia: Carguero de hoja negra (*M. Sánchez S. et al. 802*, *879*), Quïbojïdujecu (Muinane name) (*M. Sánchez S. et al. 802*, *879*).

Notes — *Guatteria atabapensis* is well recognizable by its coriaceous, obscurely veined leaves, with submarginal loops quite far removed from the margins (4–7 mm), in combination with very short pedicels and short stipes. It looks quite similar to *G. maguirei*, which is also confined to savannas, but it differs from the latter by much shorter pedicels and larger leaves.

Some sterile Colombian collections identified by Murillo A. & Restrepo (2000) as *G. atabapensis* deserve further attention. They differ from the remainder by verruculose leaves, but are otherwise quite similar. It concerns the following:

Colombia, **Amazonas**, Río Caquetá, Isla Mariñame, *M. Sánchez S. et al. 802* (COAH, U); Río Caquetá, Isla Morocoy, *M. Sánchez S. et al. 879* (COAH, U). **Caquetá**, Sierra de Chiribiquete, 560 m, *P. A. Palacios et al. 2627* (U).

Fig. 15 *Guatteria atabapensis* Aristeg. ex D.M.Johnson & N.A.Murray. Flowering branch (*Wurdack & Adderley 42759*; isotype US).

17. *Guatteria australis* A.St.-Hil. — Fig. 16; Plate 1h; Map 6

Guatteria australis A.St.-Hil. (1825) 37; R.E.Fr. (1939) 306, t. 1. — *Guatteria australis* var. *glabrata* Mart. (1841) 26. — Type: *A.C.F.P. de Saint-Hilaire 1452* (holo P 3 sheets), Brazil, São Paulo, Itararé ('bords of Tararé'), Jan. 1817.

Guatteria gomeziana A.St.-Hil. (1825) 36; R.E.Fr. (1939) 319. — Type: *A.F.C.P. de Saint-Hilaire 560* (holo P 2 sheets; iso K), Brazil, Minas Gerais, Rio Piracicaba ('Itajuru de São Miguel de Mato Dentro'), Jan.–Feb. 1817.

Guatteria lutea A.St.-Hil. (1825) 37; R.E.Fr. (1939) 322. — *Guatteria flava* A.St.-Hil. ex Mart. (1841) 27, nom. superfl. — Type: *A.F.C.P. de Saint-Hilaire 304* (holo P), Brazil, Minas Gerais, Ouro Preto ('entre Vila Rica et Antônio Pereira'), Jan. 1817.

Uvaria hirsuta Vell. (1829) 224; (1831) t. 124, nom. illeg., non *Uvaria hirsuta* Jack (1820) 46. — Type: Velloso's plate 124 (lecto, selected by Maas et al. 2011).

Uvaria monosperma Vell. (1829) 224; (1831) t. 123, nom. illeg., non *Uvaria monosperma* Lam. (1785) 596. — Type: Velloso's plate 123 (lecto, selected by Maas et al. 2011).

Guatteria hilariana Schltdl. (1834) 324; R.E.Fr. (1939) 396. — *Guatteria hilariana* f. *latifolia* Schltdl. (1834) 324. — *Guatteria hilariana* var. *latifolia* (Schltdl.) Mart. (1841) 35. — Type: *Sellow s.n.* (holo B; iso HAL), Brazil, without locality and date.

Guatteria hilariana Schltdl. f. *angustifolia* Schltdl. (1834) 324; R.E.Fr. (1939) 397. — *Guatteria hilariana* var. *angustifolia* (Schltdl.) Mart. (1841) 35. — Type: *Sellow 5943 p.p.* (holo B 2 sheets; iso HAL), Brazil, São Paulo, Santos, Apr.–July 1829.

Guatteria psilopus Mart. (1841) 27, t. 7, f. 1; R.E.Fr. (1939) 339. — Type: *Luschnath s.n.* (holo BR), Brazil, Rio de Janeiro, Teresópolis, Serra dos Orgãos, June 1834.

Guatteria acutiflora Mart. (1841) 29. — Type: *Wied zu Neuwied s.n.* (lecto BR, selected by Moraes 2013; isolecto BR, MEL), Brazil, Bahia, Nova Almeida ('crescit in silvis ad Villam Novam de Almeida'), Mar. 1816.

Guatteria nigrescens Mart. (1841) 31; R.E.Fr. (1939) 319. — *Guatteria nigrescens* Mart. var. *oblongifolia* Mart. (1841) 31. — Type: *Martius s.n.* (lecto M, selected by Fries 1939), Brazil, São Paulo, Guaratinguetá, Dec. 1817.

Guatteria densicoma Mart. (1841) 32; R.E.Fr. (1939) 309, f. 3b, t. 3. — Type: *Martius 711* (holo M; iso B, BR 4 sheets, F, G, HAL, K, NY, P), Brazil, Bahia, Ilhéus, Fazenda Almada, Dec. 1818.

Guatteria klotzschiana Mart. (1841) 32; R.E.Fr. (1939) 327, f. 5d–f. — *Cananga klotzschiana* (Mart.) Warm. (1873) 145. — Type: *Schott s.n.* (holo BR 2 sheets; iso B, F, US), Brazil, Rio de Janeiro, 'prope Tocaia'.

Guatteria odontopetala Mart. (1841) 33, t. 11; R.E.Fr. (1939) 407. — Type: *Pohl 2964* (lecto M, selected by Fries 1939; isolecto B, BR, F, G), Brazil, Minas Gerais, Manoel Pereira.

Guatteria hookeri A.St.-Hil. & Tul. (1842) 132; R.E.Fr. (1939) 342, f. 6c, d. — Type: *Gardner 306 p.p.* (holo P 3 sheets; iso BM, E, F, G, K 3 sheets, LZ, NY, OXF, S), Brazil, Rio de Janeiro, Teresópolis, Organ Mountains, banks of the River Paquequer, Mar. 1837.

Guatteria neglecta R.E.Fr. (1939) 308, f. 3a, t. 2. — Type: *Dusén 6780 p.p.* (holo S 2 sheets; iso F, K, L, MO, NY 2 sheets, P, U), Brazil, Paraná, Morretes, Jacareí ('Jacarehý'), 30 Sept. 1908.

Guatteria polycarpa R.E.Fr. [subsp. *polycarpa*] (1939) 310, t. 4. — Type: *Dusén 7414* (holo S; iso F, K, L, MO, NY, P), Brazil, Paraná, Piraquara, Roça Nova-Banhado, 30 Dec. 1908.

Guatteria polycarpa R.E.Fr. subsp. *drupacea* R.E.Fr. (1939) 311, f. 3c. — Type: *J.G. Kuhlmann RB 19677* (holo S; iso RB), Brazil, São Paulo, without locality, 26 Sept. 1922.

Guatteria glabrescens R.E.Fr. (1939) 311, t. 5. — Type: *J.G. Kuhlmann RB 4483* (holo S; iso F, G, RB 2 sheets), Brazil, Rio de Janeiro, Reserva Florestal da fábrica Alliança, 11 Jan. 1922.

Guatteria fruticosa R.E.Fr. (1939) 312, t. 6. — Type: *Löfgren 531* (holo S), Brazil, São Paulo, São José dos Campos, 14 Dec. 1909.

Guatteria dusenii R.E.Fr. (1939) 313, t. 7. — Type: *Dusén 13752* (holo S; iso L, MO), Brazil, Paraná, Guaratuba, July 1911.

Guatteria dusenii R.E.Fr. var. *subglabra* R.E.Fr. (1939) 313. — Type: *Dusén 4497* (holo S), Brazil, Paraná, Paranaguá ('Porto D. Pedro II'), 19 Apr. 1904.

Guatteria paranensis R.E.Fr. (1939) 314, t. 8. — Type: *Dusén 6780 p.p.* (holo S), Brazil, Paraná, Morretes, Jacareí ('Jacarehý'), 30 Sept. 1908.

Guatteria parvifolia R.E.Fr. (1939) 314, t. 9. — Type: *F.C. Hoehne SP 28405* (holo S; iso B, F, HB, K, MO, SP, SPF, US), Brazil, São Paulo, São Paulo, Parque do Estado, 28 Oct. 1931.

Guatteria parvifolia R.E.Fr. var. *vestita* R.E.Fr. (1939) 315. — Type: *Sellow 211* (holo B; iso K), Brazil, São Paulo, without locality and date.

Guatteria salicifolia R.E.Fr. [var. *salicifolia*] (1939) 316, t. 10, f. 3d. — Type: *Glaziou 7508* (holo B; iso C, K, MG, P), Brazil, Rio de Janeiro, Rio de Janeiro, Tijuca, 21 Dec. 1874.

Guatteria salicifolia R.E.Fr. var. *erosa* R.E.Fr. (1939) 316. — Type: *Dusén s.n.* (holo S; iso F), Brazil, Paraná, Morretes, Jacareí ('Jacareý'), 1914.

Guatteria curvinervia R.E.Fr. (1939) 317, t. 11. — Type: *Frazão 8667* (holo S; iso RB), Brazil, São Paulo, Barretos, Dec. 1917.

Guatteria mosenii R.E.Fr. (1939) 321. — Type: *Mosén 4002* (holo S), Brazil, São Paulo ('Serra do Caracol'), 15 Dec. 1875.

Guatteria asterantha R.E.Fr. (1939) 323, t. 12. — Type: *Mexia 5485* (holo S; iso BM, F 2 sheets, G, K, NY, U, US), Brazil, Minas Gerais, Viçosa ('road to Cajurý, Canella'), 750 m, 7 Jan. 1931.

Guatteria acutipetala R.E.Fr. (1939) 324, t. 13. — Type: *Ule 3962* (holo B), Brazil, Rio de Janeiro, Teresópolis, Jan. 1897.

Guatteria reflexa R.E.Fr. (1939) 329. — Type: *Glaziou 5725* (holo S; iso B, C, F, K, P, R, RB), Brazil, Rio de Janeiro, Niterói, Morro da Viração, 28 July 1870.

Guatteria silvatica R.E.Fr. (1939) 330. — Type: *Peckolt 151* (holo BR), Brazil, Rio de Janeiro, Cantagalo ('Canta Gallo'), 1857.

Guatteria blanchetiana R.E.Fr. (1939) 331, t. 14. — Type: *Blanchet 2114* (holo G 6 sheets; iso B, BM, F, FI, K 2 sheets, MO, NY, P 2 sheets, W), Brazil, Bahia, Ilhéus, Fazenda Almada, 1835.

Guatteria dimorphopetala R.E.Fr. (1939) 333, f. 5c. — Type: *Sellow 175* (holo B), Brazil, between Vitoria (Espírito Santo) and Bahia.

Guatteria clavigera R.E.Fr. (1939) 334, f. 5g, h. — Type: *Koscinsky 214* (holo S; iso SP), Brazil, São Paulo, São Paulo, Serra da Cantareira, 15 Dec. 1933.

Guatteria riedeliana R.E.Fr. (1939) 339, f. 6a, b. — Type: *Riedel 424* (holo S; iso LE, NY, U), Brazil, Bahia, Castelnovo, Nov. 1821.

Guatteria penduliflora R.E.Fr. (1939) 341, t. 15. — Type: *Allemão e Cysneiro s.n.* (holo G 2 sheets), Brazil, Rio de Janeiro, without locality, 1860.

Guatteria minarum R.E.Fr. (1939) 346, t. 16. — Type: *Mexia 5130* (holo S; iso BM, C, F 2 sheets, G, K, NA, NY, U), Brazil, Minas Gerais, Viçosa ('Fazenda Paraiso'), 1 Oct. 1930.

Guatteria hilariana Schltdl. var. *cuneata* R.E.Fr. (1939) 397. — Type: *Burchell 3366* (holo K; iso K, P), Brazil, São Paulo, Santos, Montserrat, NE part of island São Vicente, 3 Nov. 1826.

Guatteria hilariana Schltdl. var. *verruculosa* R.E.Fr. (1939) 397. — Type: *Mosén 3337* (holo S; iso B, P, US), Brazil, São Paulo, Santos, Baturoca, 25 Jan. 1875.

Guatteria sordida R.E.Fr. [var. *sordida*] (1939) 532. — *Guatteria sordida* var. *stenopetala* R.E.Fr. (1939) 533, t. 39 p.p. — Type: *Lund 959* (syn C), Brazil, São Paulo, Mogi ('Mugy'), Nov. 1833 and *Lund s.n.* (syn C), Brazil, São Paulo, without locality and date.

Guatteria sordida R.E.Fr. var. *lancifolia* R.E.Fr. (1939) 533, t. 39 p.p. — Type: *Riedel 1689 p.p.* (holo S; iso K), Brazil, São Paulo, Mogi ('prope Muji'), Nov. 1833.

Guatteria sordida R.E.Fr. var. *ovalis* R.E.Fr. (1939) 533, t. 39 p.p. — Type: *Riedel 1689 p.p.* (holo S; iso B, K, P), Brazil, São Paulo, Mogi ('prope Muji'), Nov. 1833.

Guatteria tenuis R.E.Fr. (1939) 535, t. 40. — Type: *Mexia 5482* (holo S; iso BM, F, G, K, U), Brazil, Minas Gerais, Viçosa, Fazenda do Deserto, 690 m, 5 Jan. 1931.

Tree 1–26 m tall, 6–20 cm diam; young twigs densely covered with appressed, rarely erect hairs, soon glabrous. *Leaves*: petiole 2–8 mm long, 1–3 mm diam; lamina narrowly elliptic to elliptic, 5–20 by 1.5–7 cm (leaf index 2–6.7(–9.5)), chartaceous, not verruculose, shiny, blackish green to blue above, pale brown to brown below, sparsely covered with appressed hairs to glabrous above, densely covered with appressed hairs to glabrous below, base acute to attenuate, apex acute to acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins distinct, 8–20 on either side of primary vein, raised above, smallest distance between loops and margin 2–4 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; flowering and fruiting pedicels 15–60 mm long, 1–3 mm diam, densely covered with appressed, brown hairs to glabrous, articulated at 0.2–0.3 from the base, bracts 3–5, soon falling, elliptic to narrowly elliptic, 4–7(–20) mm long; flower buds broadly ovoid; sepals free, broadly triangular, 5–10 by 5–7 mm, reflexed, outer side glabrous; petals cream in vivo, narrowly elliptic to elliptic, 10–38 by 5–20 mm, outer side densely covered with appressed, brown hairs to glabrous; stamens c. 2 mm long, connective shield hairy. *Monocarps* 15–45, green, maturing red to purple-black in vivo, black in sicco, ellipsoid, 6–15 by 5–7 mm, glabrous, apex apiculate (apiculum c. 0.5 mm long), wall c. 0.5

mm thick, stipes 10–30 by 1 mm. *Seed* ellipsoid, 6–10 by 5–7 mm, dark brown, rugulose, raphe not distinct from rest of seed.

Distribution — Brazil (Bahia, Espírito Santo, Goiás, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo).

Habitat & Ecology — In non-inundated and periodically inundated, often Atlantic forest, or cerrado, on clayey to sandy soil. At elevations of 0–2000 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Brazil: Cambuí (*P. Rosa RB 81409*), Imbira (*H.C. Lima 3405*), Pindaíba.

Note — *Guatteria australis* is very variable, generally being characterized by medium-sized leaves (5–20 by 1.5–7 cm) with

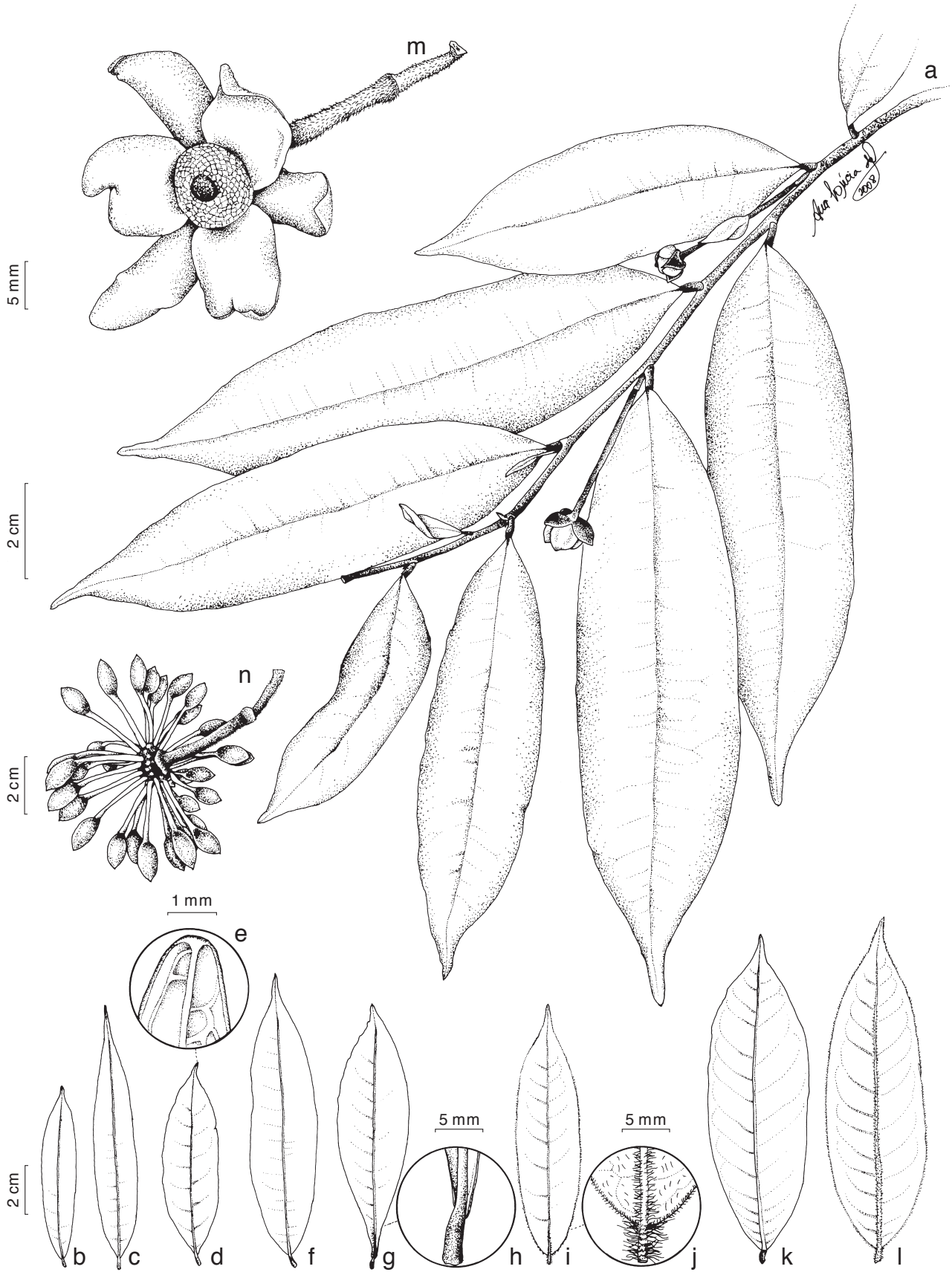
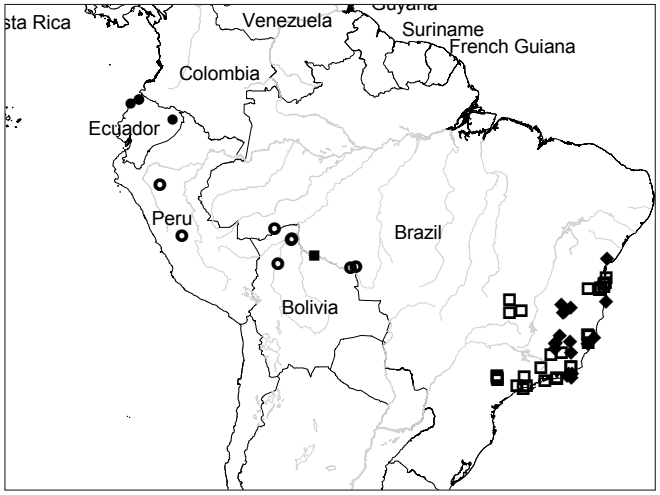
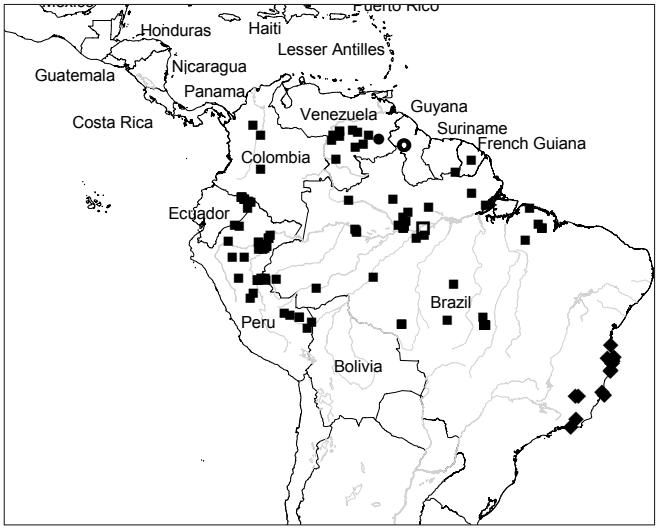


Fig. 16 *Guatteria australis* A.St.-Hil. a. Flowering habit; b–d, f, g, i, k, l. leaves; e. leaf apex; h, j. leaf base; m. flower; n. fruit (all from Lobão et al. (2011) f. 1).



Map 6 Distribution of *Guatteria australis* (□), *G. beckii* (⊙), *G. beniensis* (■), *G. brevipetiolata* (●) and *G. campestris* (◆).



Map 7 Distribution of *Guatteria auyantepuiensis* (●), *G. ayangannae* (⊙), *G. blepharophylla* (■), *G. campinensis* (□) and *G. candolleana* (◆).

acute to acuminate apex and flowering pedicels often around 50 mm long. The indument is also highly variable, individuals with glabrous branches and leaves (e.g., *Dusén 13746* from Guaratuba, Paraná) occurring in the same area as individuals with a dense hair cover on branches and the lower side of leaves (e.g., *Barbosa 556*, also from Guaratuba, Paraná). *Guatteria acutiflora* was recently added to the synonymy of *G. australis* (Lobão et al. 2012). *Guatteria acutiflora* supposedly differs from the latter by rounded leaf bases (Von Martius 1841), but, as Lobão found a rounded leaf base in several specimens of *G. australis* as well, she sees no justification for keeping the two species apart. The name *G. acutiflora* DC (De Candolle 1817) is cited in reference to *G. acutifolia* Dunal and is an orthographic variant (art. 60.1 ICBN).

18. *Guatteria auyantepuiensis* Maas & Westra, *sp. nov.* — Fig. 17, 13d; Map 7

Foliis sparse verruculosis, coriaceis, apice obtusis vel breviter acuminatis, floribusque breviter pedicellatis distincta. — Typus: *F. Cardona 2619* (holo US; iso VEN, not seen), Venezuela, Bolívar, Auyantepui ('Cerro Auyan'), Alto Caroni, en pequeños bosques abrigados, lugares rocosos, 1600 m, Jan. 1949.

Tree c. 6 m tall, diam not recorded; young twigs densely covered with appressed hairs, soon glabrous. *Leaves*: petiole c. 5 mm long, 2 mm diam; lamina elliptic, 9–12 by 3–4 cm (leaf index 2.5–3), coriaceous, sparsely verruculose, shiny, dark brown above, brown below, glabrous above, sparsely covered with appressed hairs below, base acute to attenuate, apex obtuse to shortly acuminate (acumen to c. 5 mm long), primary vein impressed above, secondary veins distinct, 8–10 on either side of primary vein, raised above, smallest distance between loops and margin 2–4 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels c. 5 mm long, 2 mm diam, densely covered with appressed hairs, articulated at c. 0.3. from the base, bracts c. 6, soon falling, not seen; flower buds not seen; sepals basally connate, broadly ovate-triangular, 4–5 by 5–6 mm, appressed, outer side densely covered with appressed hairs; petals colour in vivo unknown, oblong-elliptic, 10–12 by 5–6 mm, outer side densely covered with erect and appressed hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* and *seed* not seen.

Distribution — Venezuela (Bolívar).

Habitat & Ecology — In non-inundated forest, on rocky outcrops. At an elevation of c. 1600 m. Flowering: January; fruiting: not known.

Vernacular names — Not recorded.

Note — *Guatteria auyantepuiensis* has been recorded by Johnson and Murray (see Steyermark et al. 1995) as *Guatteria sp. A*. It belongs to sect. *Mecocarpus* and shares some features with *G. meliodora* (e.g., the shiny and sparsely verruculose and obtuse to shortly acuminate leaves), but the leaves are much smaller (9–12 vs 22–35 cm long), have fewer secondary veins (8–12 vs 18–20) and the flowers have shorter pedicels (5 vs 10–20 mm long). Moreover, the leaves are quite distinct by the strongly reticulate tertiary venation.

19. *Guatteria ayangannae* Scharf & Maas — Map 7

Guatteria ayangannae Scharf & Maas in Scharf et al. (2005) 565, f. 2. — Type: *Clarke et al. 9819* (holo U 2 sheets; iso BRG, NY 4 sheets), Guyana, Potaro-Siparuni Region, Upper Potaro River, near camp, Mt Ayanganna, 650 m, 3 July 2001.

Tree 5–7 m tall, c. 10 cm diam; young twigs densely covered with erect, orange-brown hairs to c. 1.5 mm long, soon glabrous. *Leaves*: petiole 7–14 mm long, 1–2 mm diam; lamina elliptic to obovate, 10–17 by 4–6 cm (leaf index 2.1–2.9), coriaceous, scabridulous particularly below, pale to creamy brown above, brown below, glabrous above, densely covered with appressed, orange-brown to silvery hairs to c. 1.5 mm long below when young, soon becoming sparsely covered with appressed hairs to c. 0.5 mm long, then becoming glabrous, base acute, apex acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 9–14 on either side of primary vein, flat above, smallest distance between loops and margin 2–4 mm, tertiary veins flat above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 5–15 mm long, c. 2 mm diam, fruiting pedicels to c. 15 mm long, c. 3 mm diam, densely covered with appressed, orange-brown hairs, articulated at 0.3–0.5 from the base, bracts 5–6, the lower bracts soon falling, elliptic-ovate, c. 2 mm long, the 2 upper ones often persisting till flowering time, often foliaceous, elliptic to narrowly elliptic, 7–40 mm long, to 15 mm wide; flower buds broadly ovoid, slightly pointed; sepals basally connate, triangular, 9–10 by 5–6 mm, often reflexed, apex strongly acuminate, outer side densely covered with appressed, orange-brown hairs; petals greenish yellow or yellow in vivo, elliptic to ovate, 14–18 by 6–10 mm, outer side densely covered with appressed, orange-brown hairs; stamens c. 2 mm long, connective shield hairy. *Monocarps* 2–8, green to reddish brown in vivo, black in sicco, narrowly ellipsoid, 15–23 by 4–6 mm, sparsely covered with appressed hairs to c. 0.5 mm long to glabrous, apex nipple-

Fig. 17 *Guatteria auyantepuiensis* Maas & Westra. Flowering branch (*F. Cardona 2619*; holotype US).

shaped (nipple c. 2 mm long), wall 0.3–0.5 mm thick, stipes 5–8 by 1–2 mm. *Seed* narrowly ellipsoid, 13–15 by 4–5 mm, dark, shiny brown, smooth to slightly pitted, raphe not distinct from rest of seed.

Distribution — Guyana (Mt Ayanganna).

Habitat & Ecology — In dense, mixed evergreen forest with *Dicymbe*, *Pentaclethra*, *Clusia*, *Socratea* and *Euterpe*, on grey, alluvial sand, sandstone, peat, or lateritic soil. At elevations of 650–1120 m. Flowering: June to August; fruiting: June to August.

Vernacular names — Not recorded.

Note — *Guatteria ayangannae* is only known from Mt Ayanganna in Guyana. It is a very beautiful species, particularly by its young vegetative and floral parts which are densely covered with appressed, orange-brown hairs up to c. 1.5 mm long. The acuminate, basally fused sepals and the presence of foliaceous bracts are other features by which this species is easily recognized.

20. *Guatteria beckii* Maas & Westra, *sp. nov.* — Fig. 13e, f, 18; Plate 2c; Map 6

Guatteriae maypurensis affinis sed differt monocarpiis ellipsoideis nec anguste oblongo-ellipsoideis, praeterea pedicellis brevioribus et sepalis longioribus distincta. — Typus: *Beck & Haase 9895* (holo U 2 sheets; iso G, LPB, M, MO, NY), Bolivia, La Paz, Prov. Iturralde, Luisita, wet savanna W of Río Beni, 180 m, 22 Feb. 1984.

Shrub, small tree, or liana 3–7 m tall, diam not recorded; young twigs sparsely to rather densely covered with erect and some appressed hairs, soon glabrous. *Leaves*: petiole 3–10 mm long, 1–3 mm diam; lamina narrowly elliptic, 10–17 by 4–6 cm (leaf index 2.5–3.7), chartaceous, not verruculose, shiny, grey to greyish brown above, brown below, glabrous above, sparsely covered with appressed hairs to glabrous below, base acute, sometimes obtuse, apex acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 10–15 on either side of primary vein, raised above, indistinctly loop-forming, smallest distance between loops and margin 3–4 mm, tertiary veins raised above, often distinctly reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; pedicels 15–20 mm long, c. 1 mm diam, fruiting pedicels to c. 2 mm diam, sparsely to densely covered with erect hairs, articulated at 0.2–0.3 from the base, bracts 5–6, soon falling, only most basal bract seen, broadly triangular-ovate, 1–1.5 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 5–8 by 5–6 mm, reflexed, outer densely covered with appressed hairs; petals yellow to greenish brown in vivo, obovate, 15–25 by 7–15 mm, outer side densely covered with appressed, greyish hairs; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* 25–75, green, maturing black in vivo, black in sicco, ellipsoid, 7–11 by 4–6 mm, sparsely covered with appressed hairs, apex apiculate (apiculum c. 0.5 mm long), wall c. 0.2 mm thick, stipes 6–15 by c. 1 mm. *Seed* ellipsoid, 6–10 by 4–5 mm, pale to dark shiny brown, pitted, raphe raised.

Distribution — Bolivia (Beni, Santa Cruz), Peru (Junín), Brazil (Acre, Amazonas).

Habitat & Ecology — In floodplain forest, terra firme forest, wet savannas, or secondary roadside vegetation, on clayey soils (the collections from Brazil). At elevations of 150–250 (–1100) m. Flowering: January, February, May, July; fruiting: February, May, July, September.

Vernacular names — Not recorded.

Other specimens examined. Bolivia, **Beni**, Río Yata, c. 40 km SW of Guayaramirim, *Anderson & McPherson 11916* (U); Prov. Moxos, 3 km S of Puerto Palomo, 255 m, *Meneces & Terceros 335* (U); Prov. Vaca Diez, 1 & 2 km at SW edge of Riberalta, 230 m, *Solomon 7652* (MO,U); Prov. Vaca Diez, Riberalta, 170 m, *Solomon 16789* (G, LPB, MO, OWU, U, WU). **Santa Cruz**, Parque Nacional Noel Kempff, Praina Boliviana, near artificial beach of Pimenteira, 150 m, *Arroyo et al. 2638* (U); Parque Nacional Noel Kempff, Lago Caiman, 220 m, *Garvizu & Fuentes 370* (U). – Brazil, **Acre**, Mun. Rio Branco, between km 22 and 37of the Rio Branco-Porto Velho Highway, near Iquiri igarapé, 8 Feb. 1979, *Albuquerque et al. 1341* (U). **Rondônia**, Porto Velho, km 60–64 of road Guajará-Mirim to Abunã, *Carreira et al. 497* (NY, U). – Peru, **Junín**, Manto, km 20 W of Yaupi, 1100 m, 11 July 1961, *Woytkowski 6530* (MO, U).

Notes — *Guatteria beckii* is named after our friend and collegue Dr. Stephan Beck who has been and still is a very active collector and stimulator of botanic research in Bolivia.

Guatteria beckii, a small shrub, tree, or even liana ('vine'), occurs in the Bolivian states of Beni and Santa Cruz, the Peruvian state of Junín, and the adjacent Brazilian states of Acre and Amazonas where it mostly inhabits wet savannas or floodplain forests. It is recognizable by a distinct reticulate tertiary venation on the upper side of the leaves and by seeds with a very distinct raphe, a feature rarely seen in *Guatteria*.

It might be confused with *G. maypurensis*, another savanna inhabiting species occurring in Bolivia, but in the latter the leaves are often folded lengthwise in dry condition, and the pedicels are shorter while the sepals are longer (pedicels 15–20 mm vs 15–50 mm in *G. maypurensis* and sepals 5–8 vs 3–4 mm).

21. *Guatteria beniensis* Maas & Westra, *sp. nov.* — Fig. 13g, 19; Map 6

Ramulis glabris foliis nitidis costa in facie adaxiali elevata (nec impressa) et pedicellis pro ratione longis monocarpiis breviter stipitatis distincta. — Typus: *Nee 34593* (holo NY 2 sheets), Bolivia, Beni, Prov. Itenez, S side of Río Guapore, 'Campo Verde', c. 15 km ESE of Costa Marques (the Brazilian state of Rondônia), 150 m, 31 Mar. 1987.

Shrub 1.5 m tall, diam not recorded; young twigs glabrous, but new growth densely covered with erect, brown hairs to c. 1.5 mm long. *Leaves*: petiole 3–5 mm long, c. 1 mm diam; lamina narrowly oblong-elliptic, 8–10 by 2.5–3 cm (leaf index 2.6–4), coriaceous, not verruculose, shiny, greyish brown above, pale brown below, glabrous above and below, but very young leaves densely covered with erect to appressed, brown hairs to c. 1 mm long on both sides, base acute to obtuse, apex bluntly acute, primary vein slightly raised above, secondary veins distinct, 10–12 on either side of primary vein, slightly raised above, smallest distance between loops and margin 1–2 mm, tertiary veins slightly raised above, reticulate. *Flowers* only seen in fruiting stage, solitary, in axils of leaves; fruiting pedicels c. 40 mm long, 1 mm diam, glabrous or covered with some scattered erect and appressed hairs, articulated at 0.2–0.3 from the base, bracts 4–5 (?), soon falling, not seen. *Monocarps* (young ones) c. 50, colour in vivo not recorded, black in sicco, ellipsoid, 5–6 by 2 mm, rather densely covered with appressed and erect, brown hairs, apex pointed, stipes c. 2 by 1 mm. *Seed* not seen.

Distribution — Bolivia (Beni).

Habitat & Ecology — In very flat natural, grazed savanna with scattered shrubs and short, tortuous trees, with evidence of fires, and with large termite mounds, on black, silty soil. At an elevation of c. 150 m. Flowering: unknown; fruiting: March.

Vernacular names — Not recorded.

Note — Occurring in wet savannas in the Bolivian state of Beni, *G. beniensis* is recognizable by shiny leaves in which the primary vein is raised on the upper side, by relatively long pedicels (c. 40 mm long) and shortly stipitate monocarps. The leaves and young twigs are completely glabrous, but in a very young stage they are covered by a very dense indument of brown hairs.

Fig. 18 *Guatteria beckii* Maas & Westra. Flowering branch (*Beck & Haase 9895*; holotype U).

Fig. 19 *Guatteria beniensis* Maas & Westra. Fruiting branch (*Nee 34593*, holotype NY).

Fig. 20 *Guatteria blainii* (Griseb.) Urb. Flowering branch (*Ekman 5920*, S).

22. *Guatteria bernardii* R.E.Fr. — Map 5

Guatteria bernardii R.E.Fr. (1960) 23. — Type: *Bernardi 6534* (holo NY; iso S), Venezuela, Bolívar, Calzeta de la Botella, 150 m, 14 Apr. 1957.

Tree 8–15 m tall, 15–40 cm diam; young twigs densely covered with erect, brown hairs, soon glabrous. *Leaves*: petiole 2–3 mm long, c. 1 mm diam; lamina narrowly elliptic, 9–15 by 1.5–3 cm (leaf index 3.2–6), chartaceous, not verruculose, shiny, greyish brown to brown above, brown below, glabrous above, densely covered with erect to appressed hairs below, base acute, apex acuminate (acumen 10–15 mm long), primary vein flat above, secondary veins distinct, 12–14 on either side of primary vein, raised above, smallest distance between loops and margin 1–2 mm, tertiary veins flat above, reticulate. *Flowers* in 1(–2)-flowered inflorescences, in axils of leaves; flowering and fruiting pedicels 15–20 mm long, c. 1 mm diam, densely covered with erect to appressed hairs, articulated at 0.3–0.5 from the base, bracts 5–6, soon falling, not seen; flower buds globose to depressed globose; sepals basally connate to free, broadly ovate-triangular, 4–5 by 4–5 mm, reflexed, outer side rather densely covered with erect to appressed hairs; petals pale greenish yellow, oblong-elliptic to obovate-oblong, 10–20 by 4–5 mm, outer side densely covered with erect to appressed hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* c. 25 (?), colour in vivo not recorded, brown in sicco, ellipsoid, 8–10 by 5 mm, glabrous, apex apiculate (apiculum < 1 mm long), wall c. 0.2 mm thick, stipes 4–7 by 1 mm. *Seed* ellipsoid, 7–8 by 4–5 mm, brown, smooth, raphe raised.

Distribution — Venezuela (Bolívar).

Habitat & Ecology — In secondary growth ('en malezas'). At elevations of 80–150 m. Flowering: February, April; fruiting: April.

Vernacular name — Venezuela: Majaguillo (*Ll. Williams 11248*).

Uses — Venezuela: 'Se usa la madera para construcción de casas como viguetas, horcones y la cáscara fibrosa para cordaje' (*Ll. Williams 11248*).

Other specimen examined. Venezuela, **Bolívar**, La Unión, Medio Caura, 80 m, 14 Feb. 1939, *Ll. Williams 11248* (F 2 sheets).

Note — *Guatteria bernardii*, only twice collected in the Venezuelan state of Bolívar, has been placed in the synonymy of *G. schomburgkiana* by Johnson (in Steyermark et al. 1995) and also until recently by us. It is quite distinct, however, differing from the latter by longer pedicels (≥ 15 mm vs ≤ 10 mm in *G. schomburgkiana*) and by the absence of hairs on the connective shield so characteristic for the latter.

23. *Guatteria blainii* (Griseb.) Urb. — Fig. 13h, 20; Plate 2f, g; Map 8

Guatteria blainii (Griseb.) Urb. (1905) 239; R.E.Fr. (1939) 476, f. 25a. — *Asimina blainii* Griseb. (1866) 3. — Type: *Wright 1103* (holo GOET; iso B, F, G, GH, GOET, K, MO, P), Cuba, Guantánamo, near Monte Verde ('Prope villam Monte Verde dictam, Cuba orientali'), Jan. 1859.

Asimina neglecta Griseb. (1866) 3. — *Uvaria para-neglecta* M.Gómez (1894) 42.

Uvaria viridiflora Sessé & Moç. (1894), non (Splitg. ex de Vriese) Walp., non Ruiz & Pav. ex G.Don — Type: a collection by *Sessé & Moçiño* (syn FI, G 2 sheets), Puerto Rico, 'Rio Piedras ad Praedium de la Campana interjectis. Floret Septembri'. We have studied the following 3 syntype collections:

1. A collection in the Webb-Herbarium, which forms part of the herbarium in Florence (FI). The specimen is annotated on the right side as '*Uvaria viridiflora* Pavon' at the bottom to the right 'Herb. Webbianum' ... 'Ex Herb. Pavon' ... and above it in Sessé & Moçiño's handwriting '*Uvaria viridiflora* ... NE' Although 'NE' would mean Mexico ('Nueva Espana') we are convinced that the specimen belongs to *Guatteria blainii*, which it clearly resembles, and that the specimen was collected in Puerto Rico, as indicated in the original description.
2. and 3. In the Geneva Herbarium (G) we recently found 2 specimens, one '*Uvaria viridiflora* N..31-7 ... and at the right bottom a blue label with 'Nueva España ... Herb. Pavon' and a second collection '*Waria viridiflora* Peru ... Pavon ... vide *Unona aromatica*'. Both collections certainly belong to *G. blainii* and were already identified as such by Robert Fries (in 1931 and 1937, respectively).

Guatteria moralesii (M.Gómez) Urb. (1905) 240; R.E.Fr. (1939) 479. — *Uvaria moralesii* M.Gómez (1887) 30. — Type: *Wright 1851 p.p.* (syn B, BM, G, GOET, K, P, S, W), Cuba, without location.

Guatteria neglecta (Griseb.) P.Wilson ex Léon & Alain (1951) 178, non R.E.Fr. — Type: *Wright 1851 p.p.* (holo GOET), Cuba, without location.

Guatteria cubensis Bisse (1975) 3. — Type: *Bisse & Areces HFC 16920* (holo HAJB; iso HAJB, JE), Cuba, Oriente, Palenque, Cuchillas del Toa, Cayo Fortuna, Río Toa, Apr. 1970.

Tree or shrub 3–20 m tall, 10–50 cm diam; young twigs rather densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 4–6 mm long, 1–2 mm diam; lamina elliptic to obovate or narrowly so, 4–10(–12) by 1.5–4 cm (leaf index 1.5–5), coriaceous, not verruculose, shiny, dark green to brown above, pale green to brown below, glabrous above and below (sometimes sparsely covered with appressed hairs along the primary vein), base acute to obtuse, extreme base slightly attenuate, margins sometimes revolute, apex emarginate to shortly acuminate (acumen 2–5 mm long), primary vein flat to impressed above, secondary veins distinct, 8–13 on either side of primary vein, strongly raised above, smallest distance between loops and margin c. 1 mm, tertiary veins strongly raised above, reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets, or pseudoterminal due to abortion of shoot apex, exceptionally terminal; bracts 4–8, soon falling, not seen except for occasional foliaceous bract to c. 21 by 7 mm; pedicels 15–50 mm long, 1–2 mm diam, fruiting pedicels to c. 60 mm long, to c. 3 mm diam, sparsely covered with appressed hairs to glabrous, articulated at 0.1–0.2 from the base; flower buds depressed ovoid, initially slightly pointed; sepals basally connate, broadly ovate-triangular, 4–7 by 3–5 mm, reflexed, outer side sparsely covered with appressed hairs to glabrous, margins often thickened and densely hairy; petals green, maturing yellow in vivo, elliptic, 7–20 by 4–10 mm, outer side densely covered with appressed hairs; stamens 1–1.5 mm long, connective shield hairy to papillate. *Monocarps* 10–25, green when young in vivo, black in sicco, ellipsoid, 7–18 by 4–7 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.6 mm thick, stipes 0–2(–5) by 1–3 mm. *Seed* ellipsoid, 7–17 by 4–7 mm, dark brown, smooth, sometimes longitudinally grooved, rarely also transversely grooved, raphe not distinct from rest of seed.

Distribution — Greater Antilles: Cuba, Hispaniola (the Dominican Republic and Haiti), Puerto Rico.

Habitat & Ecology — In wet, montane, broad-leaved forest, on lateritic to serpentine soil. At elevations of 1000–1400 m.

Map 8 Distribution of *Guatteria blainii* (●), *G. caribaea* (✪), *G. chiriquiensis* (■), *G. costaricensis* (□), *G. crassivenia* (◆) and *G. darienensis* (✱).

Flowering: throughout the year; fruiting: January, April to July, November, December.

Vernacular names — Cuba: Pimienta malagueta. Dominican Republic: Yaya (*Mera 2054*), Yaya francesa (*J. Jiménez 4627*).

Field observations — In *Zanoni et al. 30964* from the Dominican Republic the flowers are 'banana scented, with a scent of *Cananga odorata*'.

Notes — *Guatteria blainii*, the only species of *Guatteria* occurring in the Greater Antilles, is a quite variable species to be recognized by relatively small and shiny leaves with the secondary veins strongly raised on the upper side, and by sessile or shortly stipitate monocarps.

There is a lot of variation in the seed structure of *G. blainii*, much more than in other species of the genus. The seeds vary from smooth, longitudinally grooved, to transversely grooved.

Leaves of sterile material are different from leaves of fertile material, they are larger and long-acuminate, with a petiole ranging from 7–12 mm by 2 mm and the lamina from 8–11 cm by 4–5 cm.

24. *Guatteria blepharophylla* Mart. — Map 7

Guatteria blepharophylla Mart. (1841) 38; Maas & Westra (2011) 115, f. 1a, 2, 3a, pl. 1a, b. — *Guatteriopsis blepharophylla* (Mart.) R.E.Fr. (1934) 110, t. 6; Maas et al. (2007) 644. — Type: *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, G 2 sheets, LE, M, NY, P, W), Brazil, Amazonas, Rio Negro, towards confluence with Rio Solimões, May 1851.

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

Guatteria brevicuspis R.E.Fr. (1939) 491, f. 28e, f. — Type: *Krukoff 5589* (holo S; iso BM, F, G, K, M, MO, NY 2 sheets, RB, S, U 2 sheets, US), Brazil, Acre, Rio Purus, near mouth of Rio Macauã ('Macauhan'), tributary of Rio Iaco ('Yacu'), 21 Aug. 1933.

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

Guatteria sp. 1 Chatrou et al. (1997) 109.

Shrub or tree, 2–13(–25) m tall, to c. 10(–30) cm diam; young twigs densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 8–13 mm long, 2–4 mm diam; lamina narrowly obovate-oblong to narrowly ovate-oblong, rarely elliptic, 15–35 by 3.5–8.5(–12) 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 to c. 1 mm long below, base long-attenuate, sometimes acute to 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, tertiary veins slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 4–10(–20) mm long, 1–3 mm diam, fruiting pedicels rarely to c. 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, yellow-orange or cream in vivo, rhombic-ovate to 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 to 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, rugulose to rugose, longitudinally and transversely grooved, raphe not distinct from rest of seed.

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

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

Vernacular names — Brazil: Envira-preta (*H.C. & R.P. Lima 2718*), Envireira (*Rodrigues 534*), Pindaíba-preta (*Marimon 51*). Peru: Anonilla (*Freitas 7*, *Ruiz & Melendez 1344*), Carahuasca amarilla (*Tello 2999*), Hicoja (*Schunke V. 7688*), Hicoja negra (*Schunke V. 4294*, *8674*), Huasca anonilla (*Vásquez 12285*), Huasca hicoja (*Schunke V. 7844*), Icoja (*Rimachi Y. 4175*), Tortuga (*Plowman 2537*). Venezuela: Kunguate (Yekuana) (*Aymard C.* & *Fernández 7324*), Kunwatö (Yekuana) (*Ang. Fernández 5266*).

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

Guatteria blepharophylla is a variable species. Characteristically it has densely to rather densely verruculose leaves with a long-attenuate base, and it is found as such particularly in Amazonian Brazil and Venezuela. 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.

25. *Guatteria brevipetiolata* Maas & Westra — Map 6

Guatteria brevipetiolata Maas & Westra in Erkens et al. (2008) 478, f. 4. — Type: *T.D. Pennington et al. 14941* (holo U 2 sheets; iso K 2 sheets), Ecuador, Esmeraldas, Anchayacu, Eloy Alfaro, Mayronga, 100–250 m, 14 Apr. 1994.

Guatteria sp. 5 Chatrou et al. (1997) 110.

Tree or shrub 3–20 m tall, to c. 30 cm diam, slash orange-brown; young twigs densely covered with erect and appressed, pale brown, somewhat curly hairs. *Leaves*: petiole 2–5 mm long, 1–3 mm diam; lamina narrowly oblong-elliptic to narrowly elliptic, 16–28 by 7.5–10 cm (leaf index 2.6–3.2), chartaceous, not verruculose, shiny, green above, green below, sparsely covered with erect and appressed, pale brown, somewhat curly hairs above, rather densely covered with erect and appressed, pale brown, somewhat curly hairs below, base obtuse, sometimes oblique, apex acute to shortly and very gradually, bluntly acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 10–15 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* 1–2-flowered inflorescences in axils of or on leafless branchlets; pedicels 30–55 mm long, 1–2 mm diam, densely to rather densely covered with erect and appressed, pale brown, somewhat curly hairs, articulated at 0.1–0.2 from the base, bracts 4–6, soon falling; flower buds not seen; sepals free, ovate, 6–7 by 4–5 mm, spreading to reflexed, outer side densely covered with appressed hairs; petals pale green, greenish brown or greenish red in vivo, oblong-elliptic to narrowly oblong-elliptic, 13–20 by 5–11 mm, outer side densely covered with mostly appressed hairs; stamens 1.5–2 mm long, connective shield papillate, hairy or glabrous. *Monocarps* and *seed* not seen (but on label of *Aulestia & Gonti 1736*: 'frutos jovenes cremas').

Distribution — Ecuador (Esmeraldas, Napo).

Habitat & Ecology — In primary forest, on red, clayey soil. At elevations of 60–250 m. Flowering: February to April; fruiting: February (?).

Vernacular name — Ecuador: Oitahumo (*Aulestia & Gonti 1736*).

Note — *Guatteria brevipetiolata* can be recognized by a short petiole, an oblique and obtuse leaf base, a bluntly acuminate leaf apex and long-pedicellate flowers.

26. *Guatteria campestris* R.E.Fr. — Fig. 21; Map 6

Guatteria campestris R.E.Fr. (1939) 402. — Type: *Glaziou 14466* (holo B; iso BR, C, G, K, P), Brazil, Minas Gerais, Araçuaí ('Arassuahy').
Guatteria reticulata R.E.Fr. (1939) 324, f. 4b–d. — Type: *Schwacke 9155* (holo B), Brazil, Minas Gerais, Ouro Preto, 7 Feb. 1893.
Guatteria xylopioides R.E.Fr. (1939) 459, f. 21g. — Type: *Glaziou 13401* (holo B; iso K, P), Brazil, Rio de Janeiro, Cabo Frio, Feb. 1882.

Tree 3–18(–22) m tall, 13–35 cm diam; young twigs densely to sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 5–10 mm long, 1.5–2 mm diam; lamina narrowly elliptic, sometimes elliptic, 7–21 by 2–6(–9) cm (leaf index 1.8–6), chartaceous, not verruculose, pale brown to brown on both sides, sparsely covered with appressed hairs to glabrous above, densely covered with appressed hairs to glabrous below, base obtuse, rarely acute, apex acute, primary vein impressed above, secondary veins distinct, 12–16 on either side of primary vein, raised above, angle of secondary vein with primary vein 40–55°, smallest distance between loops and margin 1–2 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 5–25 mm long, 1–2 mm diam, fruiting pedicels 2–3 mm diam, densely to sparsely covered with appressed, brown hairs, finally glabrous, articulated at 0.2–0.3 from the base, bracts 2–4, soon falling, 2–4 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 5–6 by 5–6 mm, reflexed, outer side glabrous; petals cream in vivo, ovate, 10–25 by 6–10 mm, outer side densely covered with appressed, brown hairs; stamens c. 1 mm long, connective shield hairy. *Monocarps* c. 15, green when young in vivo, black in sicco, ellipsoid, 12–14 by 8 mm, glabrous, apex apiculate (apiculum < 1 mm long), wall c. 0.8 mm thick, stipes 2–5 by 1 mm. *Seed* ellipsoid, 12–14 by 5 mm, orange-brown, pitted to rugulose, raphe raised.

Distribution — Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro).

Habitat & Ecology — In non-inundated, Atlantic rain forest or cerrado, on clayey soil. At elevations of 0–1050 m. Flowering: throughout the year; fruiting: January, April, May, October, November.

Vernacular names — Brazil: Araticum (*Ramalho & Rodrigues 1594*), Conde (*Piratininga 14*), Imbuí (*R. Guedes 2280*, *Piratininga 14*).

Note — *Guatteria campestris* is distinct by mostly narrowly elliptic leaves with an obtuse base, with secondary veins forming an angle of 40–55° to the primary vein, which is a narrow angle for the genus. It resembles *G. australis* in the size and the shape of the leaves (narrowly elliptic to elliptic). However, *G. australis* has secondary leaf veins forming an angle of 70–90° with the primary vein.

27. *Guatteria campinensis* (Morawetz & Maas) Erkens & Maas — Map 7

Guatteria campinensis (Morawetz & Maas) Erkens & Maas (2008) 405. — *Guatteriella campinensis* Morawetz & Maas (1984) 20, f. 1, 2. — Type: *Morawetz & D. Coêlho 31-24883* (holo INPA; iso INPA 2 sheets, U, WU), Brazil, Amazonas, km 165 of new road from Manaus to Itacoatiara, 24 Aug. 1983.

Tree 12–15 m tall, to c. 15 cm diam; young twigs densely covered with a velutinous indument of erect, brown, long-persistent

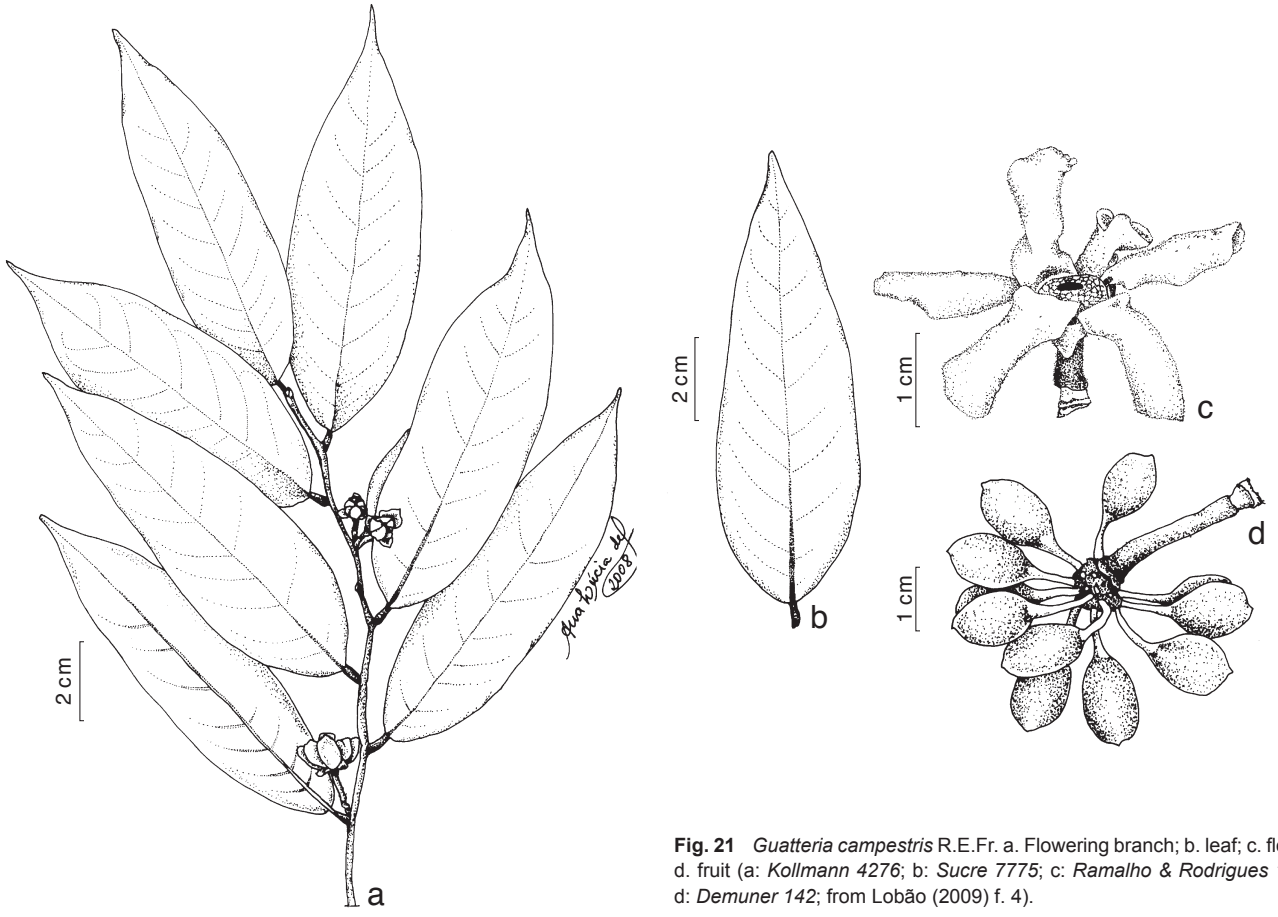


Fig. 21 *Guatteria campestris* R.E.Fr. a. Flowering branch; b. leaf; c. flower; d. fruit (a: *Kollmann 4276*; b: *Sucre 7775*; c: *Ramalho & Rodrigues 1594*; d: *Demuner 142*; from Lobão (2009) f. 4).

hairs. *Leaves*: petiole 2–5 mm long, 3–5 mm diam; lamina narrowly elliptic to narrowly obovate, 15–32 by 7–12 cm (leaf index 2.2–2.7), chartaceous, not verruculose, shiny, dark brown above, brown below, sparsely covered with erect, brown hairs above, the primary vein densely so, rather densely covered with a velutinous indument of erect, brown hairs below, base obtuse to subcordate and almost stem-clasping, apex acute to acuminate (acumen to c. 10 mm long), primary vein impressed above, secondary veins distinct, 20–26 on either side of primary vein, impressed above, more or less forming a marginal vein, at a smallest distance of 2–3 mm from the margin, tertiary veins impressed above, percurrent. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 5–7 mm long, c. 3 mm diam, fruiting pedicels 5–11 mm long, 4–5 mm diam, densely covered with a velutinous indument of erect, brown hairs, articulated at c. 0.5 from the base, bracts not seen, not countable; flower buds not seen; sepals free, broadly ovate-triangular, c. 10 by 10 mm, appressed, outer side densely covered with a velutinous indument of erect, brown hairs; petals brown or golden yellow in vivo, ovate, c. 20 by 13 mm, outer side densely covered with a velutinous indument of erect, brown hairs; stamens 1–2 mm long, connective shield hairy. *Monocarps* 25–50, brown when ripe in vivo, brown in sicco, ellipsoid, 15–20 by 6–13 mm, densely covered with a velutinous indument of erect, brown hairs, apex rounded, wall 0.5–1{–2} mm thick, stipes 2–5 by 2–5 mm. *Seed* ellipsoid, 14–17 by 4–7 mm, pale greyish bown, rugulose and longitudinally and transversely grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Brazil (Central Amazonas).

Habitat & Ecology — In campina forest, on white sand. At elevations below 100 m. Flowering: August; fruiting: August, December.

Vernacular names — Not recorded.

Note — *Guatteria campinensis*, formerly put in the genus *Guatteriella*, shares the velutinous indument of most parts and the leaf venation with *G. trichocarpa*. It differs from that species, however, by its much shorter petioles (2–5 vs 5–10 mm) and the lack of verruculose structures in the leaves.

28. *Guatteria candolleana* Schltdl. — Fig. 22; Map 7

Guatteria candolleana Schltdl. (1834) 325; R.E.Fr. (1939) 342. — *Cananga candolleana* (Schltdl.) Warm. (1873) 145. — Type: *Sellow 5442 p.p.* (holo B; iso BR, G, K), Brazil, Rio de Janeiro, Sumidouro.

Guatteria hilariana Schltdl. var. *pallescens* R.E.Fr. (1900) 15. — Type: *Glaziou 3855* (lecto B, selected by Lobão in Maas et al. 2011; isolecto C, K, P), Brazil, Rio de Janeiro, Rio de Janeiro, Jacarepaguá, 29 Sept. 1869.

Treelet or shrub 0.7–4 m tall, 5–17 cm diam; young twigs densely covered with erect, brown hairs to c. 2 mm long, soon glabrous. *Leaves*: petiole 2–4 mm long, c. 1 mm diam; lamina elliptic, 5–15 by 2–4 cm (leaf index 2–4.3), chartaceous, sparsely verruculose, dark brown, brown below, glabrous above, densely covered with erect, brown hairs to c. 2 mm long to glabrous below, base cordate, sometimes obtuse, apex acute to shortly acuminate (acumen c. 5 mm long), primary vein impressed above, secondary veins distinct, 9–13 on either side of primary vein, raised above, smallest distance between loops and margin c. 1 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; flowering and fruiting pedicels 12–60 mm long, 0.5–1 mm diam, densely to sparsely covered with erect, brown hairs, articulated at 0.2–0.3 from the base, bracts 2–4, soon falling, 5–8 mm long; flower buds broadly ovoid; sepals free, broadly ovate-triangular, 2–6 by 2–5 mm, reflexed, outer side densely to sparsely covered with erect, brown hairs; petals cream or yellow in vivo, elliptic, 10–30 by 8–12 mm, outer side densely covered with erect to appressed, brown hairs; stamens c. 2 mm long, connective

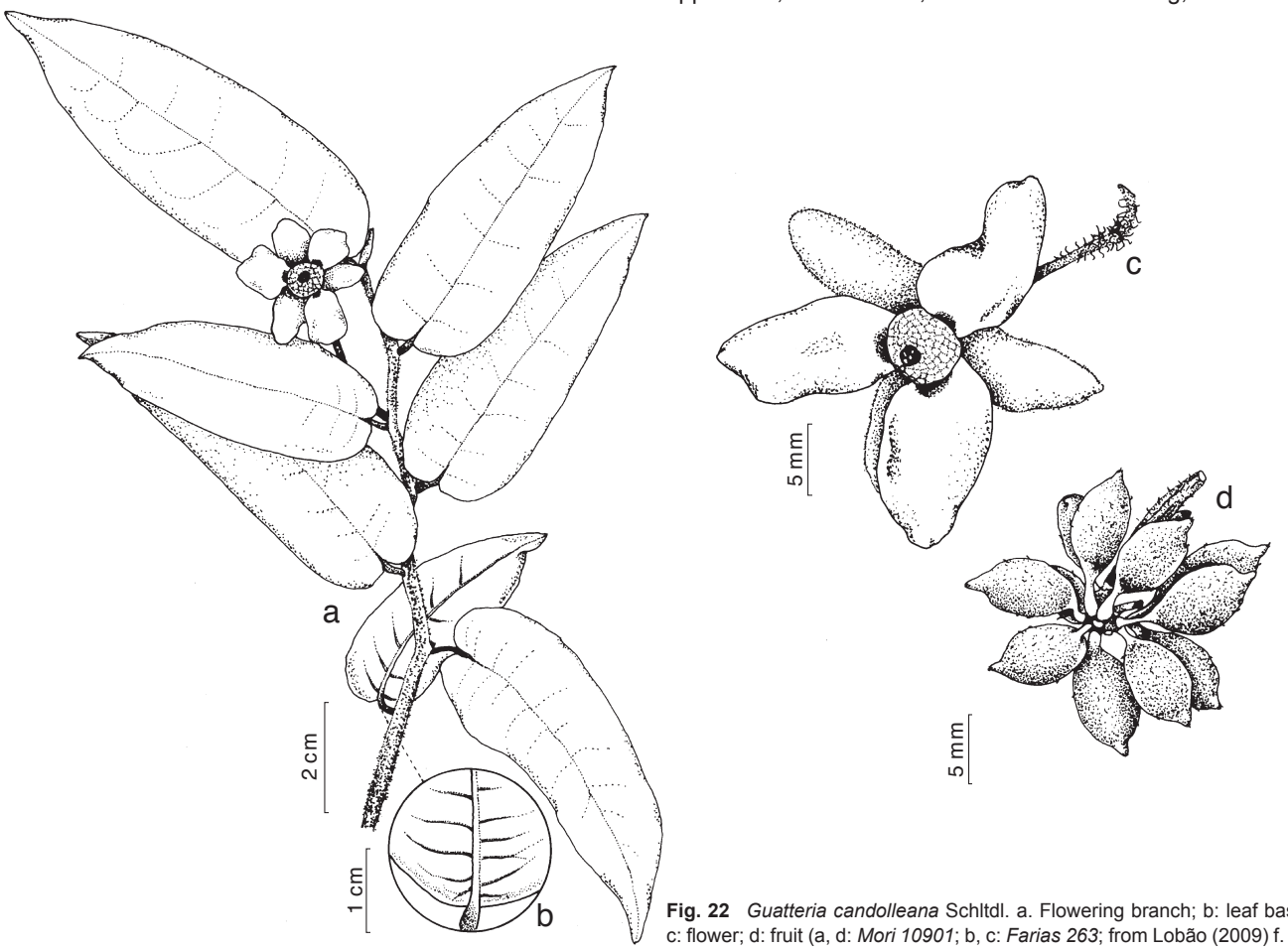


Fig. 22 *Guatteria candolleana* Schltdl. a. Flowering branch; b: leaf base; c: flower; d: fruit (a, d: *Mori 10901*; b, c: *Farias 263*; from Lobão (2009) f. 4).

shield papillate. *Monocarps* c. 10, blackish purple in vivo, black in sicco, ellipsoid, 7–10 by 4–5 mm, glabrous, apex apiculate (apiculum c. 1 mm long), wall 0.1–0.3 mm thick, stipes c. 5 by 0.5–1 mm. *Seed* ellipsoid, 7–10 by 4–5 mm, orange-brown, pitted, raphe slightly raised.

Distribution — Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro).

Habitat & Ecology — In non-inundated, Atlantic, sometimes disturbed rain forest or cerrado, on clayey to sandy soil. At elevations of 0–380 m. Flowering: January to August; fruiting: August, October.

Vernacular names — Brazil: Pindaíba (*Eupunino 100*, *Folli 698*), Pindaíba-candoleana (*L.A.M. Silva et al. 928*), Pindaíba-da/de-capoeira (*L.A.M. Silva et al. 860*, *928*), Pindaíba-mole (*L.A.M. Silva & Brito 860*), Puruna-do-nativo (*V.C. Souza 166*).

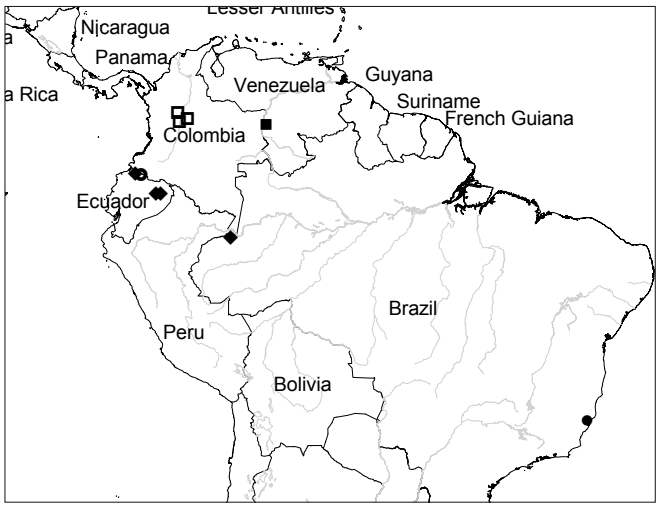
Notes — *Guatteria candolleana* is characterized by leaves with a cordate or sometimes obtuse base, densely covered with erect hairs on the lower side. It is similar to *G. australis* but that species has leaves with an acute to decurrent base.

For differences with *G. macropus* see under that species.

29. *Guatteria capixabae* Lobão & J.C.Lopes — Map 9

Guatteria capixabae Lobão & J.C.Lopes (2014) 205, f. 1. — Type: *Kollmann et al. 1948* (holo RB; iso MBML), Brazil, Espírito Santo, Santa Teresa, Valsugana Velha, Estação Biológica de Santa Lúcia, 500 m, 11 Feb. 1999.

Tree or shrub 2–6 m tall, 4–6 cm diam; young twigs glabrous. *Leaves*: petiole 4–6 mm long, 1–1.5 mm diam; lamina narrowly elliptic, rarely narrowly obovate, 7–15 by 1.5–5 cm (leaf index 2.3–5.3), chartaceous, not verruculose to densely verruculose, greyish above, dark grey below, glabrous above, glabrous or rarely sparsely covered with appressed hairs below, base attenuate, apex acuminate (1–10 mm long), primary vein flat above, secondary veins distinct, 9–18 on either side of primary vein, smallest distance between loops and margin 2–3 mm, tertiary veins reticulate, raised above. *Flowers* solitary in axils of leaves; bracts 3–4, soon falling, not seen; pedicels 8–10(–30) mm long, c. 1 mm diam, fruiting pedicels to c. 25 mm long, 1–1.5 mm diam, sparsely covered with appressed hairs to glabrous, articulated at 0.2–0.4 from the base; flower buds not seen; sepals free, deltate, c. 3 by 3–4 mm, appressed, outer side glabrous or rarely sparsely covered with appressed hairs; petals yellow in vivo, elliptic to rhombic-ovate, 10–15 by 4–8 mm, outer side densely covered with erect, grey hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* 5–7, reddish in vivo, blackish in sicco, narrowly ellipsoid, 13–17 by 4–7 mm, glabrous or rarely sparsely covered with appressed hairs, apex apiculate (apiculum c. 0.5 mm long), wall c. 0.5 mm thick; stipes 2–4 by 1–2 mm. *Seed* narrowly ellipsoid, 12–15 by 4–5 mm brown reddish, rugose.



Map 9 Distribution of *Guatteria capixabae* (●), *G. carchiana* (⊙), *G. castilloi* (■), *G. chasmantha* (□) and *G. chrysophylla* (◆).

Distribution — Brazil (Espírito Santo).

Habitat & Ecology — In non-inundated, Atlantic rain forest. At elevations of 500–850 m. Flowering: August, February; fruiting: November, March.

Vernacular names — Not recorded.

Note — *Guatteria capixabae*, endemic to the Brazilian state of Espírito Santo, is recognizable by very shortly stipitate monocarps and an attenuate leaf base. In the original description it is mentioned that the leaves are verruculose and that this species should be compared with species of sect. *Mecocarpus* (like *G. duodecima*), but the specimen we had at hand in Leiden had only very vague verruci and is in that respect completely different from the structures so typical for sect. *Mecocarpus*. In our opinion *G. capixabae* is very close to *G. stenocarpa*, endemic to the Brazilian state of Bahia, differing in shorter stipes (2–4 vs 5–10 mm) and smaller monocarps (13–17 vs 18–25 mm).

30. *Guatteria carchiana* Maas & Westra, *sp. nov.* — Fig. 23, 24a; Map 9

Foliis coriaceis, pilis erectis subtus obtectis, apice acutis, summo obtuso, monocarpiis seminibusque apice punctatis bene distincta. — Typus: *Vargas L. et al. 4242* (holo MO; iso QCNE, U), Ecuador, Carchi, Espejo, Reserva Golondrinas, path between Estación Santa Rosa and El Corazón, 1700–2050 m, 21 Jan. 2004.

Tree 10–30 m tall, diam not recorded; young twigs densely covered with erect, brown hairs to c. 1 mm long, soon glabrous. *Leaves*: petiole 3–5 mm long, c. 2 mm diam; lamina elliptic to obovate or narrowly so, 15–18 by 6–8 cm (leaf index 2.1–2.8), coriaceous, not verruculose, dull, grey above, brown below, glabrous above, densely covered with erect, brown hairs to c. 1 mm long below, base acute to obtuse, margins slightly revolute, apex bluntly acute, primary vein impressed above, keeled below, secondary veins distinct, 12–15 on either side of primary vein, raised above, smallest distance between loops and margin 2–4 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 15–20 mm long, 1–1.5 mm diam, fruiting pedicels to c. 25 mm long, 2–4 mm diam, densely to sparsely covered with erect, brown hairs, finally glabrous, articulated at 0.2–0.3 from the base, bracts 5–6, soon falling, not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 5–6 by 5–6 mm, reflexed, outer side densely covered with erect, brown hairs; petals greenish yellow to dull orange in vivo, ovate to elliptic, c. 15 by 8–10 mm, outer side densely covered with erect, brown hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* c. 75, dark red-purple to black in vivo, black in sicco, narrowly ellipsoid, 14–16 by 5–6 mm, sparsely covered with appressed hairs, soon glabrous, apex hard-pointed (apiculum c. 1 mm long), wall 0.2–0.3 mm thick, stipes 15–25 by 1 mm. *Seed* narrowly ellipsoid, c. 15 by 6 mm, brown, apex pointed, rugulose.

Distribution — Ecuador (Carchi).

Habitat & Ecology — In wet, montane forest. At elevations of 1450–2050 m. Flowering: January, May; fruiting: January, May.

Vernacular names — Ecuador: Cafesillo (*Vargas L. et al. 4242*).

Field observations — Flowers with cherimoya-like scent (*Madison et al. 4442*).

Uses — Ecuador: Wood used for form work ('Madera para encofrados').

Other specimens examined. Ecuador, **Carchi**, near Maldonado, 1450–1650 m, 24 May 1978, *Madison et al. 4442* (AAU, F, QCA, SEL, U).

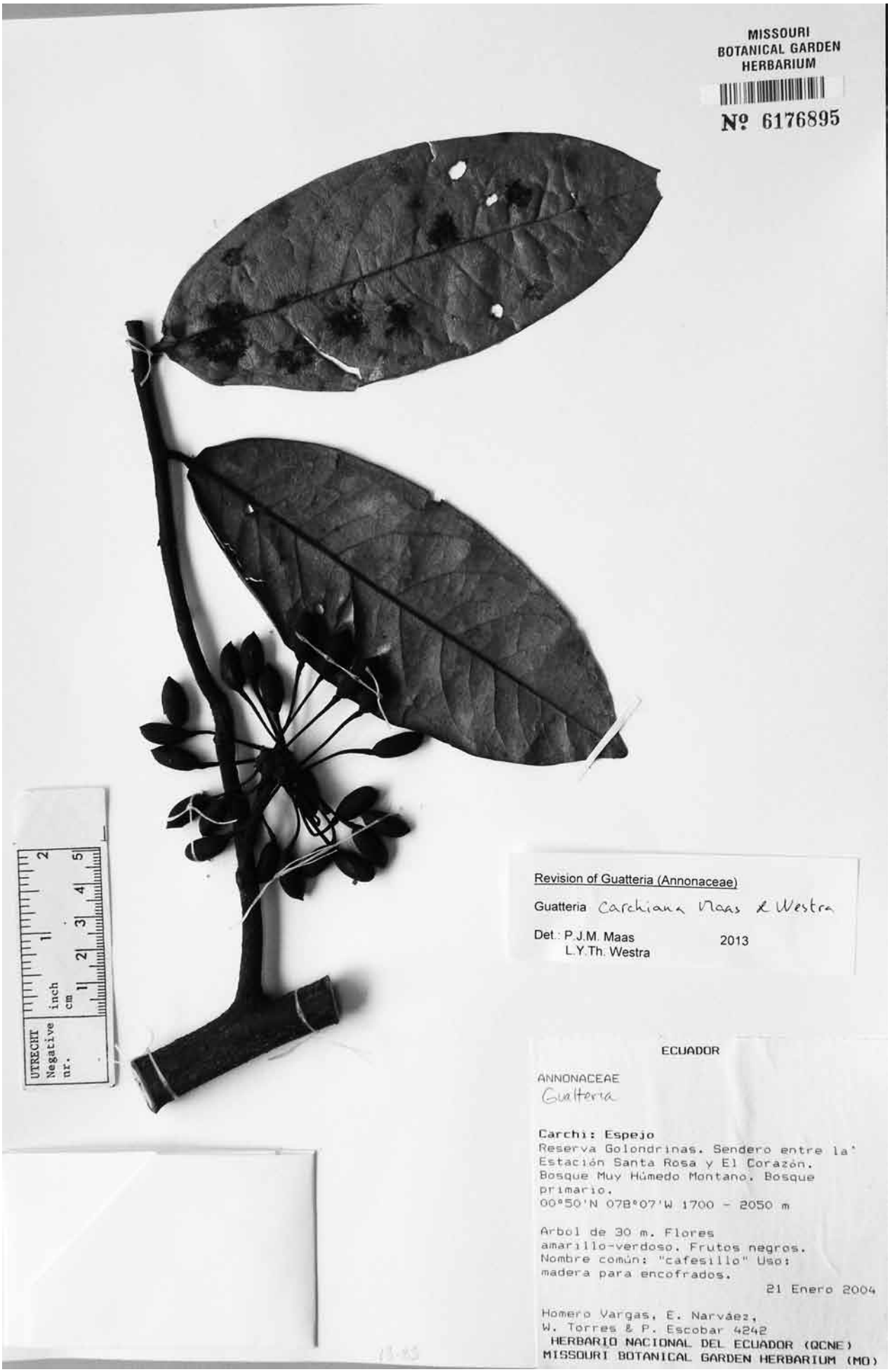


Fig. 23 *Guatteria carchiana* Maas & Westra. Fruiting branch (*Vargas L. et al. 4242*, holotype MO).

Fig. 24 a. *Guatteria carchiana* Maas & Westra. Flowers. – b. *Guatteria chiriquiensis* R.E.Fr. Fruit. – c. *Guatteria citriodora* Ducke. Fruit. – d, e. *Guatteria conspicua* R.E.Fr. d. Flowers; e. fruit. – f. *Guatteria crassivenia* N.Zamora & Maas. Detail of lower leaf surface. – g. *Guatteria delicatula* Maas & Westra. Flower pedicel with perianth and stamens gone. – h. *Guatteria dotana* N.Zamora & Erkens. Fruit (a: *Vargas L. et al. 4242*, isotype U; b: *Zamora et al. 1461*, U; c: *Mori et al. 23673*, U; d, e: *Jonker-Verhoef & Jonker 494*, U; f: *Herrera C. & Chacón 2746*, U; g: *Solomon 9282*, holotype U; h: *Estrada & Solano 1817*, MO).

Note — *Guatteria carchiana* is well recognizable by coriaceous leaves with a dense indument of erect, brown hairs on the lower side, an acute leaf apex, hard-pointed monocarps, and pointed seeds. It is probably closest to the poorly known Colombian *G. rufotomentosa*, sharing most of its indument and leaf features, but from which it differs, however, by a shorter petiole (3–5 vs 5–15 mm long), an obtuse to acute instead of attenuate leaf base, and less secondary veins (12–15 vs 15–25).

31. *Guatteria caribaea* Urb. — Plate 3a, b; Map 8

Guatteria caribaea Urb. (1905) 240; R.E.Fr. (1939) 480, f. 25b, c. — *Cananga caribaea* (Urb.) Britton in Britton & Wilson (1924) 311. — Type: *Sintenis 1535* (lecto B, selected by Fries 1939; isolecto BM, BP, G 2 sheets, GH, JE, K, L, M, NY, P, PR, S, US, WU), Puerto Rico, Sierra de Luquillo, 'in silvis montis Jiménes', June 1885.

Tree 4–40 m tall, 5–60 cm diam; young twigs rather densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 4–5 mm long, 1–3 mm diam; lamina narrowly elliptic, 8–21 by 3–8 cm (leaf index 2.2–4), chartaceous, not verruculose, dull, green to brown above and below, glabrous above, sparsely to rather densely covered with appressed hairs below but primary vein densely covered with appressed hairs, base acute, apex acuminate (acumen 10–20 mm long), primary vein impressed to flat above, secondary veins distinct, 6–12 on either side of primary vein, raised above, smallest distance between loops and margin 5–7 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; flowering and fruiting pedicels 10–25 mm long, c. 1 mm diam, sparsely covered with appressed hairs to glabrous, articulated at c. 0.2 from the base, bracts 4–5, soon falling, lower bracts very broadly ovate, c. 1 mm long, uppermost bracts one seen, broadly ovate, c. 4 mm long; flower buds depressed ovoid; sepals free, broadly to shallowly grooved, ovate-triangular, 2–4 by 3–4 mm, appressed to spreading, sparsely covered with appressed hairs; petals white or creamy white in vivo, narrowly elliptic, 10–15 by 3–5 mm, outer side densely covered with appressed hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* 5–25, green, maturing black to purple-black in vivo, black in sicco, narrowly ellipsoid, 11–20 by 5–7 mm, sparsely covered with appressed hairs, soon glabrous, apex obtusely apiculate (apiculum < 1 mm long), wall 0.3–0.5 mm thick, stipes 2–5 by 1 mm. *Seed* narrowly ellipsoid, 11–18 by 4–6 mm, dark brown, longitudinally and transversely grooved, sometimes also pitted, raphe not distinct from rest of seed.

Distribution — Lesser and Greater Antilles: Dominica, Grenada, Guadeloupe, Martinique, Montserrat, Puerto Rico, Saint Kitts and Nevis, St. Lucia.

Habitat & Ecology — In dense rain forest, on clayey loam soil. At elevations of 200–700 m. Flowering: January, March to August, November, December; fruiting: January, March to May, September, November.

Vernacular names — Bois nouè (*Jérémie 1115*), Bois violin (*Hill 25840*, *Jérémie 1115*, *Shillingford 450*), Corcho blanco (*Little Jr. 13764*), Corossol montagne (*Jérémie 1115*), Mahaut noir (*Hill 25840*), Ti-cachiman-bois (*Slane 222*), Wild soursop (*Slane 222*).

Field observations — According to *Stern & Washaussen 2595* (US) from Dominica the flowers are 'fragrant, highly aromatic'.

Notes — *Guatteria caribaea*, the only species of the genus occurring in the Lesser Antilles, is recognizable by the secondary veins which are raised on the upper side of the leaves, slender pedicels, narrowly ellipsoid monocarps on short stipes, and seeds which are mostly longitudinally and transversely grooved.

In *Stern & Wasshausen 2595* (US) the third bract from the top is more or less persisting, foliaceous, narrowly elliptic and 15–25 mm long.

Sterile material can have leaves of up to 28 by 8 cm.

32. *Guatteria castilloi* Maas & Westra — Map 9

Guatteria castilloi Maas & Westra (2010) 264, f. 5. — Type: *Castillo S. 5444* (holo VEN; iso MO), Venezuela, Amazonas, Mun. Autana, Río Sipapo, between community Monte Negro and Caldero, 250 m, 18 Aug. 1997.

Tree 8–20 m tall, diam not recorded; young twigs rather densely covered with appressed, white hairs, soon glabrous. *Leaves*: petiole 20–35 mm long, 1–2 mm diam; lamina narrowly oblong-elliptic to narrowly ovate, 12–19 by 4–8 cm (leaf index 2.4–3.7), coriaceous, not verruculose, shiny, greyish green to brown above, brown below, glabrous above, sparsely covered with appressed, white hairs below, base acute to obtuse, extreme base slightly attenuate, apex obtuse, sometimes shortly acuminate (acumen to c. 5 mm long), basal margins somewhat revolute, primary vein impressed above, secondary veins distinct, 13–15 on either side of primary vein, strongly raised above, smallest distance between loops and margin 1–2 mm, tertiary veins raised above, strongly reticulate. *Flowers* solitary in axils of leaves; pedicels 15–20 mm long, c. 1 mm diam, fruiting pedicels c. 22 mm long, 1–2 mm diam, sparsely covered with appressed, white hairs, articulated at 0.2–0.3 from the base, bracts 3–5, soon falling, upper bract c. 5 mm long; flower buds not seen; sepals free, broadly ovate-triangular, 5–6 by 5–6 mm, appressed, rigid, margins somewhat revolute, outer side sparsely covered with appressed hairs; petals green in vivo, narrowly oblong-elliptic, 13–20 by 5–8 mm, outer side rather densely to sparsely covered with appressed hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* c. 10, green in vivo, brown in sicco, ellipsoid, 13–15 by 7–10 mm, sparsely covered with appressed hairs, apex apiculate (apiculum < 0.2 mm long), wall c. 1.5 mm thick, stipes 10–12 by c. 1 mm. *Seed* not studied (abortive?).

Distribution — Amazonian Venezuela (Amazonas).

Habitat & Ecology — In black water-flooded forest ('bosque ribereño, influenciado por aguas negras'). At elevations of c. 250 m. Flowering: August to October; fruiting: October.

Vernacular names — Not recorded.

Note — *Guatteria castilloi* is unique by the combination of long petioles for the genus (20–35 mm), a raised, reticulate leaf venation, and a mostly obtuse leaf apex.

33. *Guatteria chasmantha* R.E.Fr. — Map 9

Guatteria chasmantha R.E.Fr. (1939) 513, f. 34a. — Type: *Lawrance 422* (holo S; iso A, F, G, MO, US), Colombia, Boyacá, Alto Chapón, 100 km NW of Bogotá, high forest front, 6000 ft, 9 Aug. 1932.

Tree 9–25 m tall, to c. 1.2 m diam; young twigs densely or rather densely covered with small, appressed, more or less curly hairs, soon glabrous. *Leaves*: petiole 8–15 mm long, 1.5–2 mm diam; lamina elliptic to mostly narrowly elliptic or narrowly obovate-elliptic, 12–20 by 4.5–7.5 cm (leaf index 2.4–2.9), chartaceous, sparsely or not verruculose, greyish black and more or less shiny above, brownish black to dark brown below, glabrous above, sparsely covered with small, appressed hairs to glabrous below, base acute to rounded, extreme base attenuate, apex acute to acuminate (acumen to c. 5 mm long), primary vein flat to slightly raised above, secondary veins distinct, 10–15 on either side of the primary vein, shortest distance between loops and margin 2–3 mm, tertiary

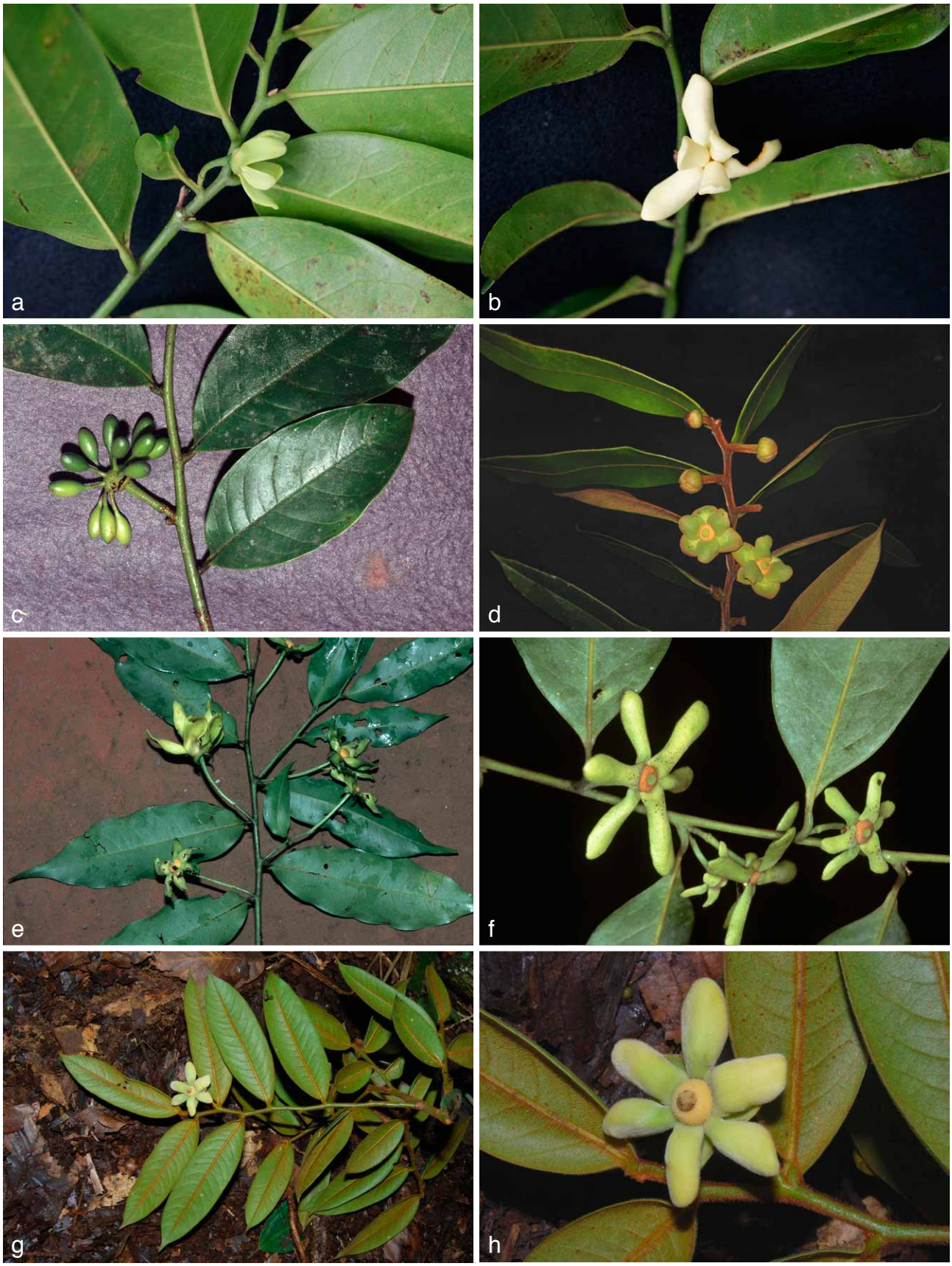


Plate 3 a, b. *Guatteria caribaea* Urb. a. Flowering branch; b. mature flower. – c. *Guatteria costaricensis* R.E.Fr. Leaves and fruit. – d. *Guatteria cuatrecasasii* Sánchez S. Flowering branch. – e. *Guatteria dolichopoda* Donn.Sm. Flowering branch and leaves. – f. *Guatteria foliosa* Benth. Flowering branch. – g, h. *Guatteria talamancana* N.Zamora & Maas. g. Flowering branch; h. flower (a, b: *Graveson et al. 3093*; c: *Maas et al. 9392*; d: *R. Cámara Leret & Copete Maturana 1743*; e: *Maas et al. 9462*; f: *Mori & Gracie 23929*; g, h: *Monro 6108*). — Photos: a, b: R.H.J. Erkens; c, e: P.J.M. Maas; d: R. Cámara Leret; f: C. Gracie; g, h: A.K. Monro.

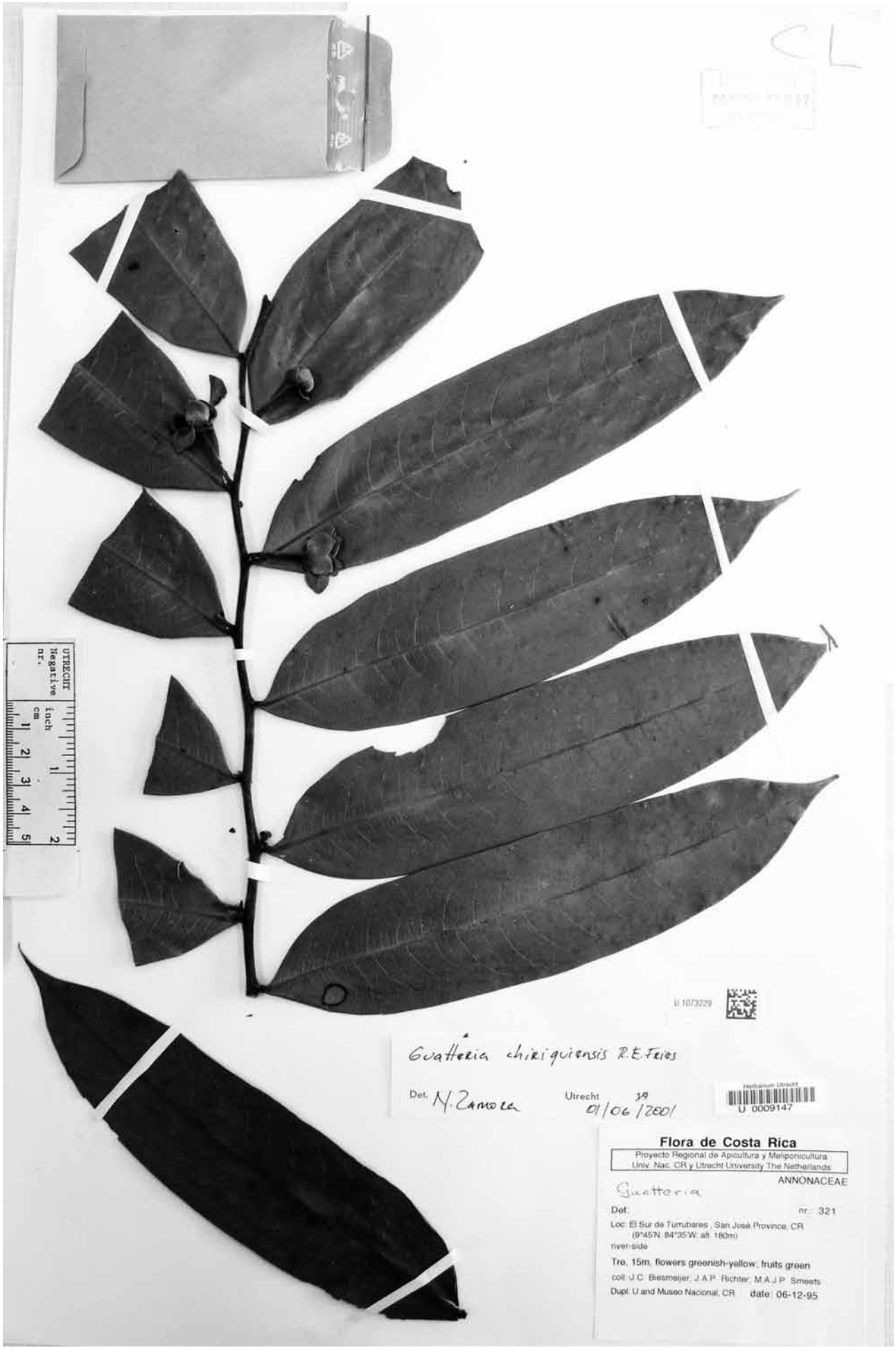


Fig. 25 *Guatteria chiriquiensis* R.E.Fr. Flowering branch (*Biesmeijer et al. 321*, U).

veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets, pedicels 12–20 by 1–1.5 mm, fruiting pedicels to c. 2 mm diam, rather densely to sparsely covered with small, appressed hairs, becoming glabrous, articulated at 0.2–0.4 from base, bracts 5–6, soon falling, not seen; flower buds not seen; sepals free, broadly ovate, 3–4 by 4–5 mm, appressed, rather densely covered with small, appressed hairs, petals yellowish green or peach-coloured in vivo, elliptic-ovate, 7–13 by 7–10 mm, inner petals distinctly smaller than outer petals, densely (base) to rather densely covered with whitish hairs, stamens c. 1.5 mm long, connective shield papillate. *Monocarps* 10–15, green, maturing black in vivo, black in sicco, glabrous, ellipsoid, 12–15 by 7–10 mm, apex acute to obtuse, wall 0.5–0.7 mm thick, stipes 1–10 by 2 mm. *Seed*: no good seeds seen inside monocarps (eaten by insects or attacked by fungus?).

Distribution — Colombia (Antioquia, Boyacá).

Habitat & Ecology — In forest and montane forest. At elevations of 1500–1900 m. Flowering: May and August; fruiting: August.

Vernacular names — Not recorded.

Note — *Guatteria chasmantha* is noteworthy by shiny almost blackish leaves in combination with short pedicels (12–20 mm long) and small sepals (3–4 mm long).

34. *Guatteria chiriquiensis* R.E.Fr. — Fig. 24b, 25; Map 8

Guatteria chiriquiensis R.E.Fr. (1948b) 11. — Type: *Pittier 5748* (holo US 4 sheets), Panama, Chiriquí, vicinity of San Felix, eastern Chiriquí, 0–120 m, Sept. 1912.

Tree 5–25 m tall, 5–25 cm diam; young twigs slightly winged, densely covered with a velutinous indument of long-persisting, erect, brown hairs. *Leaves*: petiole 1–5 mm long, 1–2 mm diam; lamina narrowly oblong-elliptic, 13–32 by 3–7 cm (leaf index 3.5–4.2), chartaceous, not verruculose, dull, greyish green above, brown to greenish brown below, rather densely covered with erect, brown hairs above, densely covered with a velutinous indument of erect, brown hairs below, base acute to obtuse, sometimes slightly oblique, apex acuminate (acumen 5–25 mm long), primary vein flat apically, becoming distinctly raised basally above, secondary veins distinct, 13–15 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2(–3)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 15–20 mm long, 1–2 mm diam, fruiting pedicels to c. 35 mm long, to c. 2 mm diam, densely covered with appressed and erect, brown hairs, articulated at 0.3–0.4 from the base, bracts 5–7, soon falling; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 5–7 by 5–7{–9} mm, appressed, outer side densely covered with appressed, brown hairs; petals yellow or cream in vivo, broadly oblong-ovate to oblong-ovate, 10–15{–25} by 10–12{–15} mm, outer side densely covered with appressed hairs; stamens 1–2 mm long, connective shield glabrous. *Monocarps* 15–40, dark purple to black in vivo, black in sicco, ellipsoid, 7–10 by 3–5 mm, sparsely covered with appressed hairs, particularly near the apical part, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 5–8 by c. 1 mm. *Seed* ellipsoid, 6–8 by 3–4 mm, dark, shiny brown, smooth to pitted, raphe impressed.

Distribution — Costa Rica, Panama.

Habitat & Ecology — In forest. At elevations of 0–500 m. Flowering: January, March, May, June, December; fruiting: August to October.

Vernacular name — Panama: Burillo (*P.H. Allen 5217*).

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

35. *Guatteria chrysophylla* Maas & Setten — Map 9

Guatteria chrysophylla Maas & Setten (1988) 252, f. 10. — Type: *Davis & Yost 1011* (holo NY; iso F, U 2 sheets), Ecuador, Napo, confluence of Quiwado and Tiwaeno Rivers, 22 Apr. 1981.

Tree 20–30 m tall, > 25 cm diam; young twigs densely covered with erect, golden brown, curly hairs. *Leaves*: petiole 15–30 mm long, 4–6 mm diam; lamina elliptic to narrowly elliptic, 20–30 by 8–15 cm (leaf index 2–2.6), coriaceous, not verruculose, dull, greyish green above, golden brown below, densely to rather densely covered with hairs on primary vein, otherwise glabrous above, densely covered with erect, golden brown, curly hairs below, base acute to attenuate, extreme base decurrent along petiole, apex acuminate (acumen c. 15 mm long), primary vein impressed to flat above, secondary veins distinct, 15–18 on either side of primary vein, raised above, smallest distance between loops and margin 0.5–1.5 mm, tertiary veins raised above, mostly percurrent. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves or leafless branchlets; pedicels 15–20 mm long, c. 2 mm diam, fruiting pedicels to c. 30 mm long, 3–6 mm diam, densely covered with erect, golden brown, curly hairs, becoming glabrous, articulated at 0.2–0.3 from the base, bracts c. 6, soon falling, not seen; flower buds ovoid, pointed; sepals free, broadly ovate-triangular, 10–13 by 7–9 mm, appressed, outer side densely covered with erect, golden brown, curly, hairs; petals colour not recorded, only seen in bud stage, outer side densely covered with erect, golden brown, curly, hairs; stamens not seen. *Monocarps* 3–20, green in vivo, black in sicco, ellipsoid to obovoid, 17–25 by 12–18 mm, surface smooth to irregularly wrinkled in sicco, subglabrous, apex rounded to acute, wall 1.5–2 mm thick, stipes 8–18 by 1.5–3 mm. *Seed* ellipsoid, 13–21 by 8–12 mm, reddish brown, rugose, raphe not distinct from rest of seed.

Distribution — Amazonian Ecuador (Napo, Pastaza), Peru (Loreto).

Habitat & Ecology — In non-inundated forest, on red soil. At elevations of 0–400 m. Flowering: May; fruiting: April, October.

Vernacular name — Ecuador: Menedowe (Tomo Upriver dialect), which means jaguar's tree (*Davis & Yost 1011*).

Uses — Ecuador: 'Bark crushed and mixed with water, rubbed over head and shoulders and fever will flee' (*Davis & Yost 1011*).

Note — *Guatteria chrysophylla* shares the indument of curly hairs, the pointed flower buds, long sepals and the large, wrinkled monocarps with *G. discolor*, a species occurring in Amazonian Bolivia, Brazil, Peru and French Guiana. It differs, however, by rugose instead of smooth seeds, the longer petioles (15–30 vs 5–10(–15) mm), a mostly percurrent tertiary venation, and the longer stipes (8–18 vs 2–10 mm).

36. *Guatteria citriodora* Ducke — Fig. 24c, 26; Map 10

Guatteria citriodora Ducke (1930) 104, t. 2, f. 3a–c; R.E.Fr. (1939) 467, f. 23a, b; Maas et al. (2007) 638. — Type: *Ducke RB 19609* (holo RB; iso B, F, G, K, NY, P, S, U, US), Brazil, Amazonas, Maués, near Rio Curucá, 4 June and 17 Dec. 1927.

Guatteria paraensis R.E.Fr. (1939) 464, f. 22c–e, syn. nov. — Type: *Ducke RB 17866* (holo S), Brazil, Pará, Belém ('Belém do Pará'), 7 Nov. 1922.

Guatteria duckeana R.E.Fr. var. *subcordata* R.E.Fr. (1948b) 10, pl. 4a. — Type: *Ll. Williams 15777* (holo US 3 sheets; iso G, NY), Venezuela, Amazonas, Capibara ('Capihuara'), Alto Casiquiare, 120 m, 3 June 1942.

Tree 2–33 m tall, 5–50 cm diam; young twigs densely covered with erect, brown hairs, finally glabrous. *Leaves*: petiole 2–7 mm long, 1.5–2 mm diam; lamina elliptic to ovate, mostly nar-

Fig. 26 *Guatteria citriodora* Ducke. Flowering branch (*Molino & Sabatier 1968*, U).

rowly so, 7–19 by 2–6.5 cm (leaf index 2–5), chartaceous, not verruculose, dull, greyish green to brown, brown below, densely to rather densely covered erect to more or less appressed hairs above when young, soon becoming glabrous, densely covered below with erect hairs, hairs simple or in bundles of 2–4, often with brown cell content, base acute, attenuate, or obtuse, apex acuminate (acumen 5–20 mm long) to acute, primary vein flat to slightly raised above, secondary veins distinct, 10–15 on either side of primary vein, raised above, smallest distance between loops and margin 2–5 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or less often on leafless branchlets; flowering pedicels 5–12 mm long, 1–2 mm diam, fruiting pedicels same length, rarely to c. 17 mm long, to c. 4 mm diam, densely covered with erect, brown hairs, articulated at 0.2–0.7 from the base, bracts 5–7, soon falling, the basal ones broadly elliptic-ovate, 1–2 mm long, the upper ones very broadly elliptic-ovate to elliptic, 5–10 mm long, exceptionally foliaceous bracts developed, elliptic, to c. 10 mm long; flower buds broadly ovoid to ovoid-conical; sepals free, broadly ovate-triangular, 3–7 by 3–7 mm, soon completely reflexed, outer side densely covered with erect, brown hairs; petals green, maturing cream to yellow tinged with some reddish in vivo, narrowly oblong-elliptic to narrowly obovate, 10–20 by 3–9 mm, outer side densely covered with erect, brown hairs; stamens 1–1.5 mm long, connective shield densely hairy. *Monocarps* 2–10, green, maturing red, purple to finally black in vivo, pale brown in sicco, ellipsoid to globose, 10–15 by 5–10 mm, sparsely covered with erect hairs, apex rounded, sometimes apiculate (apiculum to c. 1 mm long), wall c. 0.5 mm thick, stipes 0–2 by 0–1 mm. *Seed* ellipsoid, 6–8 by 5–6 mm, brown, smooth, raphe not distinct from rest of seed.

Distribution — Colombia (Antioquia, Vaupés), Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana, Peru (Madre de Dios), Brazil (Acre?, Amapá, Amazonas, Maranhão, Paraíba, Pernambuco, Rondônia, Roraima), Bolivia (Beni, Cochabamba, La Paz).

Habitat & Ecology — In non-inundated forest, rarely in gallery forest or campinarana, on sandy to clayey soil. At elevations of 0–400 m, exceptionally to 1300 m (Antioquia, Colombia). Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Brazil: Amajo-preto (*Krukoff 1753*), Envira, Envira-amarela, Laranjinha (*Ducke RB 19609*, *S. Silva & Martins 620*), Laranjinha-da-terra-firme (*Cid et al. 4249*), Maria-preta (*Miranda et al. IPB 14669*). Peru: Grau anona amarilla (*Hartshorn et al. 2858*). Venezuela: Fruta de burro (*Blanco 861*), Majagua (*Ll. Williams 15777*).

Field observations — Ducke (1930) when describing this species noted a penetrating smell of *Citrus* leaves, even in dried material ('Cette anonacée est remarquable par l'odeur pénétrante à feuilles de *Citrus* que répandent l'écorce et les feuilles; cette odeur persiste longtemps quoique moins forte, dans les échantillons secs.'). Also some more recent field reports of *G. citriodora* make mention of a noticeable fragrance, e.g., *S. Silva & Martins 620* with a spicy, *Eucalyptus*-like smell in most of the parts ('frutos imaturos e maturos con odor muito forte de eucalypto em quase toda a planta'), *Cid et al. 4249* ('folhas têm cheiro de capim-santo') and *Mori et al. 23673* ('bark with spicy aroma').

Notes — *Guatteria citriodora* together with *G. duckeana*, *G. schomburgkiana* and *G. stipitata* forms a group of four (as currently recognized) closely similar species that share short-pedicelled flowers and very shortly stipitate or sessile monocarps, or with stipes less than two times the length of the monocarp body (*G. stipitata*). The densely hairy connective shield also is a distinctive feature of this group (vs papillate or glabrous in most *Guatteria* species). In Fries's (1939) revision these species constituted the sect. *Cephalocarpus*, then comprising eight species, four of them now reduced to synonymy. See also Table 4.

Guatteria citriodora can be recognized by the erect hairs best seen on the lower side of the leaf on the primary vein and the lamina surface along the primary vein, in contrast to *G. schomburgkiana* with appressed hairs. Note, though, that hairs on the lower leaf side in *G. citriodora* may become more or less appressed towards the margin; therefore the primary vein area should be examined. Many leaf hairs in *G. citriodora* are filled with brown cell content in sicco. Also there may be some bundled hairs intermixed with simple hairs. *Guatteria citriodora* when not in fruit may become difficult to distinguish from *G. stipitata*, see under that species.

Guatteria duckeana var. *subcordata*, only known from the type collection from Amazonian Venezuela, is aberrant in having a cordate leaf base. As the indument matches *G. citriodora* fairly well we have provisionally placed it here.

37. *Guatteria clusiifolia* D.M.Johnson & N.A.Murray — Fig. 27; Map 10

Guatteria clusiifolia D.M.Johnson & N.A.Murray (1990) 599. — Type: *Tillett et al. 45009* (holo NY; iso K, MO), Guyana, Upper Mazaruni River Basin, NE side of Mt Ayanganna, 800–900 m, 2 Aug. 1980.

Tree 25–35 m tall, 40–80 cm diam; young twigs densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 10–20 mm long, 2–4 mm diam; lamina obovate, 12–16 by 6–8 cm (leaf index 1.8–2), coriaceous, scabridulous on both sides, dull, greenish brown to greyish green above, brown below, the youngest leaves densely covered with silvery, appressed

Table 4 Comparison of *Guatteria schomburgkiana* and closely resembling species.

Guatteria:	*citriodora*	*duckeana*	*schomburgkiana*	*stipitata*
Petiole length (mm)	2–7	3–10	2–10	5–10
Leaf base	acute, attenuate, obtuse	acute, attenuate, obtuse	acute, attenuate, obtuse	acute, obtuse
Leaf margins	plane	revolute basally	plane	revolute basally
Leaf apex	acute, acuminate	acuminate	acute, acuminate	acuminate
Leaf hairs (abaxially)	erect; simple, 2–more-bundled	erect; simple, (2-bundled)	appressed, (erect); simple	erect; simple, 2–more-bundled
Pedicel length (mm)	5–17	5–8	2–10(–15)	5–22
Sepal length (mm)	3–7	3–5	2–5	3–6
Monocarps nr.	2–10	10–20	5–20	5–20
Monocarp wall (mm)	0.5	1	0.1–0.2	0.3–0.6
Stipe length (mm)	0–2	0–4	0–3	5–11
Seed size (mm)	6–8 × 5–6	15 × 7*	5–8 × 5–6	7–12 × 5–7
Distribution	Col, Ven, 3Gui, Braz, Peru, Bol	C. Amaz. Braz (Manaus)	Col, Ven, 3Gui, Braz. Peru, Bol	Col, Ven, Ec, Peru
Elev. range (m)	0–400(–1300)	0	0–100	100–1200
Habitat	non-inundated forest	non-inundated forest	often savanna	non-inundated forest
Soil	sand/clay	sand	often white sand	sand/clay

Bol = Bolivia; Braz = Brazil; Col = Colombia; 3Gui = The three Guianas (Guyana, Suriname, French Guiana); Peru = idem; Ven = Venezuela; * = only one seen!

Fig. 27 *Guatteria clusiifolia* D.M. Johnson & N.A.Murray. Fruiting branch (*H.D. Clarke et al. 9745*, U).

hairs, soon glabrous above, sparsely covered with appressed hairs mainly along primary and secondary veins below, base attenuate, apex truncate, sometimes emarginate or shortly and slightly acuminate (acumen 1–3 mm long), primary vein impressed above, secondary veins indistinct, 9–17 on either side of primary vein, impressed or slightly raised above, smallest distance between loops and margin 3–4 mm, tertiary veins slightly impressed above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; pedicels 12–18 mm long, c. 1.5 mm diam, fruiting pedicels to c. 3 mm diam, densely to sparsely covered with appressed hairs, articulated at 0.2–0.4 from the base, bracts 6–7, soon falling, not seen; flower buds not seen; sepals free, broadly ovate-triangular, 3–5 by 4–6 mm, reflexed, outer side densely covered with appressed hairs; petals yellow in vivo, narrowly oblong-obovate to oblong-ovate, 14–23 by 4–12 mm, outer side densely covered with erect hairs at the base, sparsely so at the apex; stamens c. 1 mm long, connective shield papillate. *Monocarps* 5–15, green in vivo, reddish black in sicco, ellipsoid, 20–27 by 12–14 mm, sparsely covered with some appressed hairs, soon glabrous, apex rounded, wall 1.5–2 mm thick, stipes 4–6 by 3–4 mm. *Seed* narrowly ellipsoid, 16–21 by 9–10 mm, reddish black to dark, shiny brown, rugulose, raphe not distinct from rest of seed.

Distribution — Guyana (Mt Ayanganna).

Habitat & Ecology — In mixed, evergreen and fluvial forest, with *Dicymbe*, *Caryocar* and *Inga*, on brown sandy clay and lateritic soil. At elevations of 500–900 m. Flowering: August, September; fruiting: August.

Vernacular names — Not recorded.

Notes — *Guatteria clusiifolia* is well recognizable by its thick, scabridulous *Clusia*-like leaves.

Johnson & Murray (1990) placed it in sect. *Mecocarpus* near *G. dura*, with which in our view it has little affinity because of the absence of verruculi in the leaves. It is probably closest to *G. pachyphylla*, occurring in Amazonian Venezuela and Peru. For the differences with that species, see there.

38. *Guatteria confusa* Maas & Westra — Map 10

Guatteria confusa Maas & Westra in Erkens et al. (2008) 481, f. 5. — Type: *Díaz S. & Jaramillo 1478* (holo U; iso K, MO 2 sheets, WAG 2 sheets), Peru, Loreto, Prov. Maynas, Caserio de Urcumiraño, Río Napo, 120 m, 8 Oct. 1979.

Tree 4–16 m tall, diam not recorded; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 8–10 mm long, 2–3 mm diam; lamina narrowly elliptic, 17–24 by 5–9 cm (leaf index 2.9–3.4), coriaceous, not verruculose, shiny, blackish green above, pale brown below, glabrous above, sparsely covered with appressed hairs to glabrous below, base acute to obtuse, apex long-acuminate (acumen 10–35 mm long), primary vein impressed, flat or even slightly raised above, secondary veins distinct, 7–12 on either side of primary vein, raised above, smallest distance between loops and margin 3–5, tertiary veins raised above, reticulate. *Flowers* solitary in leaf axils; pedicels c. 3 mm long, c. 2 mm diam, fruiting pedicels 10–15 mm long, 2–4 mm diam, densely covered with appressed, brown hairs, becoming glabrous in fruit, articulation at c. 0.3 from the base, bracts 4–5, soon falling, not seen, flower buds depressed ovoid; sepals free, broadly ovate-triangular, 5–6 by 5–6 mm, appressed, outer side densely covered with appressed, brown hairs; petals green to yellow in vivo (too young to be measured), outer side densely covered with appressed, brownish white hairs; stamens not seen. *Monocarps* c. 20, green in vivo, black in sicco, ellipsoid, 19–23 by 8–9 mm, longitudinally wrinkled in sicco, glabrous, apex apiculate (apiculum 1–3 mm long), wall 0.5–0.7 mm thick, stipes 3–5 by 1–2 mm. *Seed* ellipsoid, 15–20 by 7–8 mm, dark brown, apex distinctly apiculate (apiculum 1–2 mm long), longitudinally and transversely grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Peru (Loreto).

Habitat & Ecology — In non-inundated forest, on clayey soil. At elevations of 120–170 m. Flowering: June, July, November; fruiting: June to August, October.

Vernacular names — Anona (*Rimachi Y. 1059*), Espintana (*Rimachi Y. 2458*, *4033*).

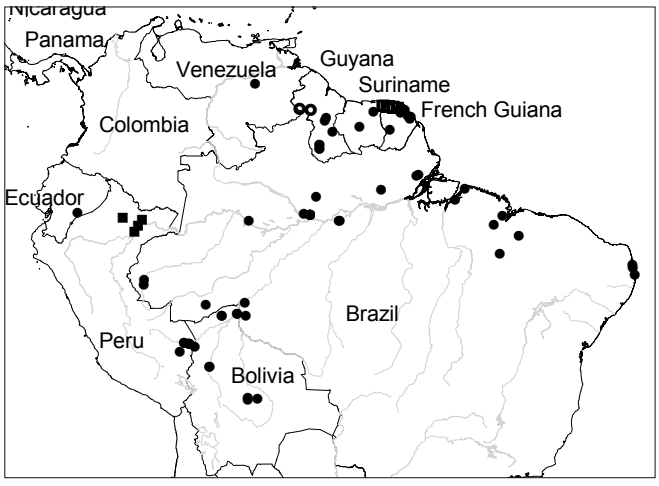
Note — The leaves *of G. confusa* are somewhat suggestive of *Ephedranthus* because of a comparatively low number of secondary veins.

39. *Guatteria conspicua* R.E.Fr. — Fig. 24d, e, 28; Map 10

Guatteria conspicua R.E.Fr. (1950b) 445, f. 1f–i. — Type: *Forest Department British Guiana 5542 = Fanshawe 2743* (holo K 3 sheets; iso FDG, K, M, NY, U), Guyana, 85 miles on Bartica-Potaro Road, 2 Nov. 1947.

Tree 4–12 m tall, 5–11 cm diam; young twigs glabrous. *Leaves*: petiole 3–8 mm long, 1–3 mm diam; lamina narrowly elliptic, 12–25 by 4–7 cm (leaf index 3–4.3), coriaceous, youngest leaves (always?) scabridulous, brown to pale brown above, brown below, youngest leaves densely covered with appressed hairs, very soon becoming glabrous on both sides, base acute to obtuse, apex acuminate (acumen 5–10 mm long), primary vein flat to slightly impressed above, secondary veins indistinct and hardly visible, 15–25 on either side of primary vein, slightly raised above, smallest distance between loops and margin 3–4 mm, tertiary veins inconspicuous and hardly visible. *Flowers* in 1(–3)-flowered inflorescences in axils of leaves or plant cauliflorous; pedicels 5–10 mm long, c. 1 mm diam, fruiting pedicels to c. 2 mm diam, glabrous, articulated at c. 0.5 from the base, bracts 6–7, soon falling, broadly ovate, basal ones c. 1 mm long, the 2 upper ones to c. 4 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, c. 5 by 4–5 mm, appressed, outer side glabrous, but the margins and apex rather densely covered with appressed hairs; petals pale greenish yellow in vivo, elliptic to broadly elliptic, 12–18 by 8–10 mm, outer side densely covered with appressed hairs; stamens 1–2 mm long, connective shield hairy. *Monocarps* 15–40, pale yellow, scarlet red to finally black in vivo, reddish brown or black in sicco, ellipsoid, 8–11 by c. 4 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 2–4 by c. 1 mm. *Seed* ellipsoid, 7–10 by c. 4 mm, dark brown, pitted to transversely grooved to rugulose, raphe not distinct from rest of seed.

Distribution — Guyana, Suriname, French Guiana.



Map 10 Distribution of *Guatteria citriodora* (●), *G. clusiifolia* (✪), *G. confusa* (■) and *G. conspicua* (□).

Fig. 28 *Guatteria conspicua* R.E.Fr. Flowering branch (*Jonker-Verhoef & Jonker 494*, U).

Habitat & Ecology — In non-inundated savanna forest or Wallaba (*Eperua falcata*) bush, on white sandy soil. At elevations of 0–100 m. Flowering: throughout the year; fruiting: January, May, November.

Vernacular names — Suriname: Djirikawa (Arawak name) (*Lanjouw & Lindeman 455*), Jari-jari (Arawak name) (*Teunissen*, *LBB 15967*), Kirikawa (Arawak name), Yariyari (Sranang name).

Notes — *Guatteria conspicua* is a very peculiar species by its scabridulous leaves with a very obscure and hardly visible venation, and by shortly pedicellate flowers. Fries described it as one of the species of sect. *Leiophyllum*.

It is noteworthy that the youngest leaves can sometimes be seen as densely verruculose, e.g., in *Sabatier 4682* (U) from French Guiana, the tiny warts becoming obscured as the scabridulous surface of mature leaves develops.

40. *Guatteria costaricensis* R.E.Fr. — Plate 3c; Map 8

Guatteria costaricensis R.E.Fr. [var. *costaricensis*] (1939) 514, f. 34b. — Type: *Oersted 146* (holo C; iso F fragment, US), Costa Rica, Cartago, Turrialba, May 1847.

Guatteria costaricensis R.E.Fr. var. *endresii* R.E.Fr. (1939) 515. — Type: *Endres 176* (holo K; iso BM, W), Costa Rica, without location.

Tree or shrub 3–10(–20) m tall, to 10–75 cm diam; young twigs often zigzagging, rather densely to sparsely covered with appressed, brown hairs, soon glabrous. *Leaves*: petiole 3–7 mm long, 1–2 mm diam; lamina narrowly elliptic, sometimes slightly falcate, 7–17 by 2–6 cm (leaf index 3–3.5), chartaceous, not verruculose, dull, drying greyish or brownish black above and below, rather densely covered with erect hairs along the primary vein above, sparsely covered with appressed, brown hairs below, base acute, apex acuminate (acumen 5–10 mm long), primary vein flat to impressed above, often keeled below, secondary veins distinct, 8–14 on either side of primary vein, raised above, smallest distance between loops and margin 1–4 mm, tertiary veins raised above, reticulate. *Flowers* in 1{–2}-flowered inflorescences in axils of leaves; pedicels 5–20 mm long, c. 1 mm diam, fruiting pedicels to c. 25 mm long, c. 2 mm diam, rather densely to finally sparsely covered with appressed, brown hairs, articulated at c. 0.2 from the base, bracts 4–7, soon falling, the basal bract elliptic, 1–2 mm long; flower buds depressed ovoid; sepals basally connate, broadly to shallowly ovate-triangular, 3–4 by 3–6 mm, reflexed, outer side sparsely covered with appressed, brown hairs, upper margins densely so; petals cream or yellow in vivo, ovate to rhombic to broadly so, 10–14 by 8–9 mm, outer side densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 30–40, green when young in vivo, black in sicco, ellipsoid, 7–10 by 4–5 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 1 mm long), wall 0.2–0.3 mm thick, stipes 8–14 by 1 mm. *Seed* ellipsoid, 8–9 by 3–4 mm, dark brown, transversely grooved to rugulose, raphe not distinct from rest of seed

Distribution — Costa Rica, Panama.

Habitat & Ecology — In premontane or montane rain forest. At elevations of 600–1950 m. Flowering: throughout the year; fruiting: April, June, November, December.

Vernacular names — Not recorded.

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

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

41. *Guatteria crassipes* R.E.Fr. — Fig. 29; Map 11

Guatteria crassipes R.E.Fr. (1939) 518, f. 34c. — Type: *Pittier 902* (holo US 3 sheets; iso S fragment), Colombia, Valle del Cauca, hills of Miraflores above Palmira, Central Cordillera, 1200–1600 m, Jan. 1906.

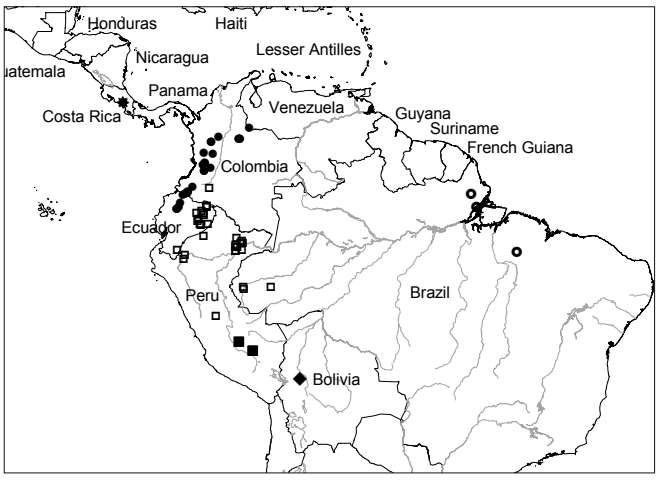
Guatteria petiolata R.E.Fr. (1939) 518, f. 34d, e, syn. nov. — Type: *Lawrance 307* (holo F; iso BM, F, G, GH, K, MO, NY, U), Colombia, Boyacá, Region of Mt Chapon, 100 miles NW of Bogotá, extreme western part of Dep. Boyacá, 1067 m ('3500 ft'), 11 July 1932.

Guatteria sp. 6 Chatrou et al. (1997) 110.

Tree 5–20 m tall, 10–40 cm diam; young twigs sparsely covered with appressed, white hairs, soon glabrous. *Leaves*: petiole 8–25 mm long, 2–4 mm diam, winged; lamina narrowly obovate to obovate, rarely elliptic, 18–47 by 7–16 cm (leaf index 2–3.1), coriaceous, densely to sparsely verruculose below at the base, rarely not verruculose, shiny, grey to greyish green to brown above, dull, pale brown or green below, glabrous above, rather densely to sparsely covered with appressed, brown hairs to glabrous below, base long-attenuate, apex obtuse to acuminate (acumen 5–15 mm long), primary vein impressed to flat above, often keeled below, secondary veins distinct, 14–20 on either side of primary vein, slightly impressed to raised above, smallest distance between loops and margin 2–4 mm, tertiary veins slightly raised above, reticulate to percurrent. *Flowers* in 1–3-flowered inflorescences in axils of the leaves or on leafless branchlets; flowering and fruiting pedicels 22–35 mm long, 1–5 mm diam, sparsely to rather densely covered with appressed, brown hairs, articulated at 0.2–0.4 from the base, bracts 4–7, soon falling, uppermost bract (in young bud) broadly elliptic, c. 2.5 mm long; flower buds broadly to depressed ovoid; sepals basally connate or free, broadly ovate-triangular, 5–9 by 5–8 mm, densely to rather densely covered with appressed, brown hairs; petals pale yellow or green in vivo, broadly ovate to ovate, 9–20 by 9–15 mm, outer side densely covered with appressed, brown hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* 20–40, green or reddish green, maturing purple or purplish black in vivo, black in sicco, ellipsoid, 11–20 by 4–10 mm, sparsely covered with appressed, brown hairs, soon glabrous, apex rounded to apiculate (apiculum 0.2–0.8 mm long), wall 0.2–1 mm thick, stipes 4–11 by 1–3 mm. *Seed* ellipsoid, 10–14 by 5–7 mm, reddish brown to brown, rugose, raphe not distinct from rest of seed.

Distribution — Colombia (Antioquia, Boyacá, Chocó, Nariño, Tolima, Valle del Cauca), Western Ecuador (Carchi, Cotopaxi, Pichincha).

Habitat & Ecology — In premontane or montane cloud forest, along the margin of the rivers and roads. At elevations of 1200–2400 m. Flowering: throughout the year; fruiting: January, February, June, August, September, December.



Map 11 Distribution of *Guatteria crassipes* (●), *G. cryandra* (⭘), *G. cuscuoensis* (■), *G. decurrens* (□), *G. delicatula* (◆) and *G. dotana* (✱).

Vernacular names — Colombia: Cargamarillo (*Mondragón 87*, *Restrepo & Mondragón 261*). Ecuador: Cargadera negra (*Tipaz et al. 1725*).

Notes — *Guatteria crassipes* is well recognizable by a combination of coriaceous narrowly obovate to obovate leaves with a long-attenuate base.

Some material collected in the Ecuadorian state of Carchi (*Freire-Fierro 2614*, *Tipaz et al. 1725*, *Rubio et al. 2199*) is aberrant in having verruculae all over the lower side of the lamina, thicker petioles (up to c. 10 mm diam) and fruiting pedicels (up to c. 8 mm diam).

42. *Guatteria crassivenia* N.Zamora & Maas, *sp. nov*. — Fig. 24f, 30; Map 8

Foliis nitidis, verruculosis, venulis omnino distincte prominentibus bene distincta. — Typus: *Herrera C. & Chacón 2746* (holo INB; iso U), Costa Rica, Limón, Cantón de Limón, El Progreso, área de suelos inundados entre 1500–1700 m, Fila Matama, 1600 m, 24 Abril 1989.

Tree c. 6 m tall, diam not recorded; young twigs densely covered with appressed, brown hairs, soon glabrous. *Leaves*: petiole 0–3 mm long, 1–2 mm diam; lamina elliptic, 6–12 by 3.5–5 cm (leaf index 1.5–2.5), chartaceous, densely verruculose along primary vein to sparsely so elsewhere, shiny, dark brown

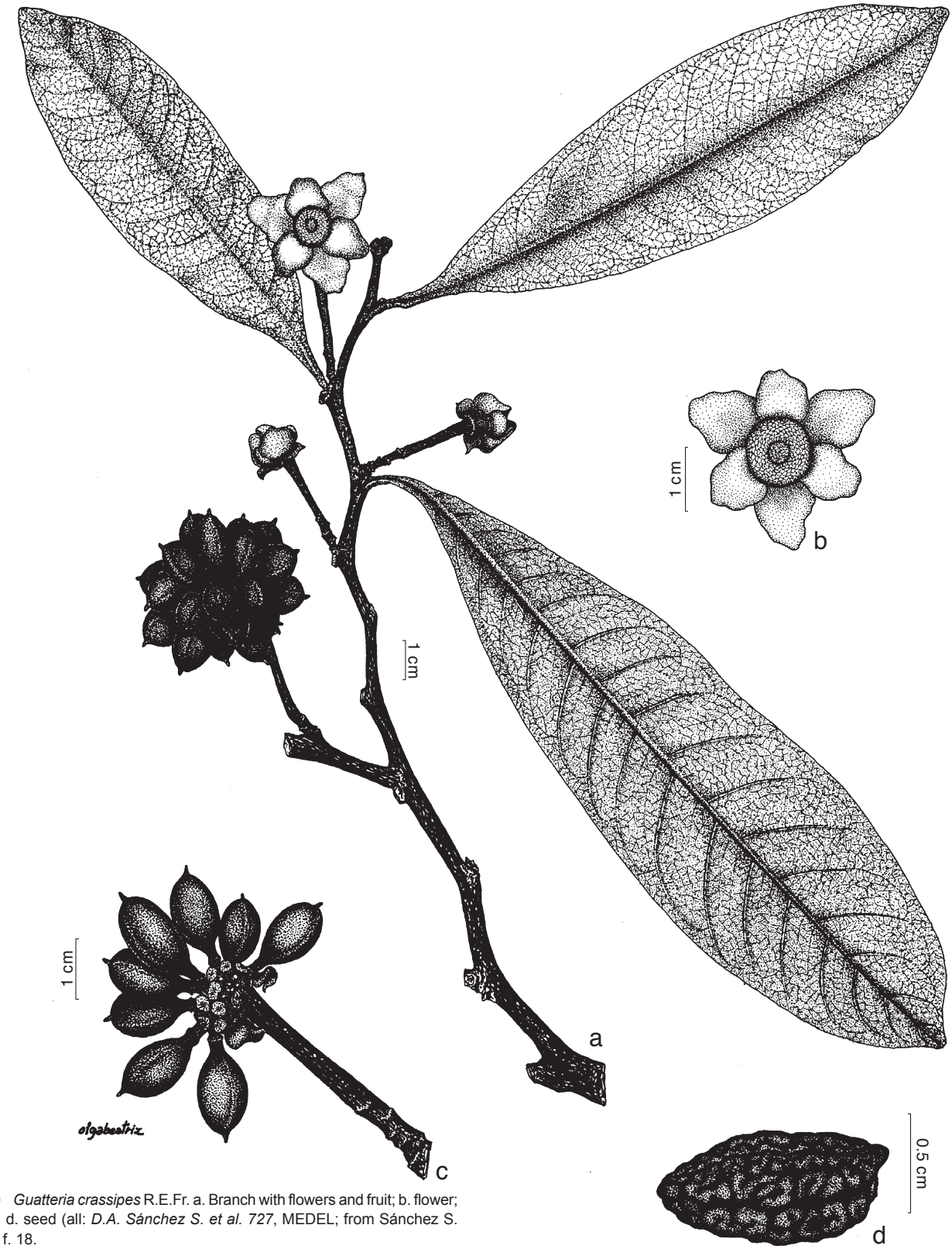


Fig. 29 *Guatteria crassipes* R.E.Fr. a. Branch with flowers and fruit; b. flower; c. fruit; d. seed (all: *D.A. Sánchez S. et al. 727*, MEDEL; from Sánchez S. (1986) f. 18.

Fig. 30 *Guatteria crassivenia* N.Zamora & Maas. Flowering branch (*Herrera C. & Chacón 2746*, isotype U).

above, brown below, densely to rather densely covered with erect, brown hairs on primary vein above, glabrous elsewhere, sparsely covered with appressed to more or less erect hairs below, base acute to slightly attenuate, apex acute to acuminate (acumen 5–15 mm long), primary vein raised above, secondary veins distinct, 12–22 on either side of primary vein, strongly raised above, smallest distance between loops and margin 1–2 mm, tertiary veins strongly raised above, reticulate. *Flowers* solitary, in axils of leaves; pedicels 10–25 mm long, c. 1 mm diam, densely to rather densely covered with appressed hairs, articulated at 0.3–0.5 from the base, bracts c. 5, soon falling, not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–6 by 4–5 mm, appressed, finally reflexed, outer side sparsely covered with appressed to more or less erect hairs; petals yellow in vivo, ovate, 10–15 by 6–11 mm, outer side densely covered with appressed hairs; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* and *seed* not seen.

Distribution — Costa Rica (Limón).

Habitat & Ecology — In wet forest. At an elevation of c. 1600 m. Flowering: April; fruiting: unknown.

Vernacular names — Not recorded.

Note — *Guatteria crassivenia*, endemic to Costa Rica and only once collected, is very easily recognized by its shiny leaves which are densely verruculose, particularly near the primary vein, by their primary vein which is raised on the upper side, and by the very prominent venation on both sides.

43. *Guatteria cryandra* Erkens & Maas — Map 11

Guatteria cryandra Erkens & Maas (2008) 404; Maas & Westra (2011) 118, f. 3b. — *Guatteriopsis kuhlmannii* R.E.Fr. (1937) 275, t. 8, not *Guatteria kuhlmannii* R.E.Fr. (1939). — Type: *J.G. Kuhlmann 2015 = RB 24361* (holo S; iso RB 4 sheets), 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 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, tertiary veins slightly raised above, reticulate. *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 to c. 5 mm long, c. 3 mm diam, densely covered with appressed, brown hairs, articulated at c. 0.2 from the base, bracts not countable with certainty, one bract seen: broadly ovate-triangular; 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 or golden yellow in vivo, broadly ovate to ovate, 10–15 by 8–10 mm, outer side densely covered with appressed, brown hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* 10–30, red to red-orange when ripe in vivo, blackish in sicco, ellipsoid, 9–12 by 4–6 mm, sparsely covered with appressed hairs, apex apiculate (apiculum 0.5–1 mm long), wall c. 0.2 mm thick, stipes 1–3 by c. 1 mm. *Seed* ellipsoid, 9–10 by 4 mm, pitted, raphe not distinct from rest of seed.

Distribution — Amazonian 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.

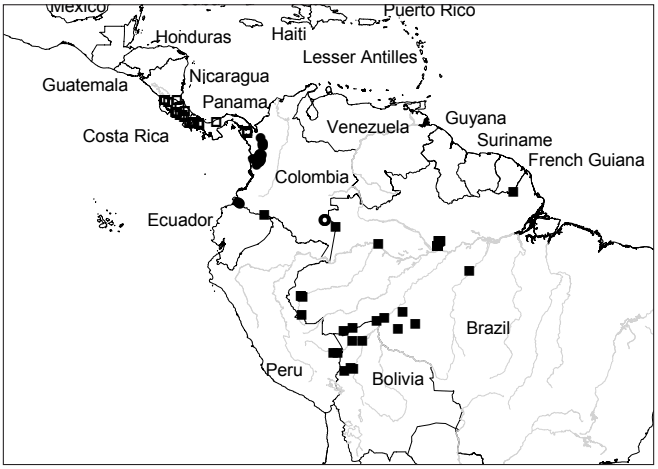
Vernacular names — Not recorded.

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 young branchlets, as well as with the shortly stipitate monocarps with stipes 1–3 mm long, and very short pedicels making the flowers appear almost sessile.

44. *Guatteria cuatrecasasii* D.Sánchez — Plate 3d; Map 12

Guatteria cuatrecasasii D.Sánchez in Maas et al. (1988) 253, f. 12. — Type: *D.A. Sánchez S. et al. 907* (holo MEDEL; iso COL, CUVC, HUA, U), Colombia, Chocó, Quibdó, Mun. Lloró, road from Yuto to Lloró, 2.8 km to the ferry, 65 m, 15 Sept. 1988.

Tree or shrub 3–35 m tall, 5–85 cm diam, often with buttresses or stilt roots; young twigs with narrow wings decurrent from petioles, densely covered with erect to appressed, brown to greyish hairs 2–3 mm long. *Leaves*: petiole 1–5 mm long, 2–4 mm diam; lamina narrowly oblong-elliptic to narrowly ovate, 10–35 by 2–7 cm (leaf index 3.5–5(–8)), subcoriaceous, densely or rarely sparsely verruculose, blackish brown to greyish above, brown below, glabrous or rarely sparsely covered with erect to appressed, brown hairs above, primary vein permanently densely to sparsely covered with erect to appressed, brown hairs above, densely covered with erect to appressed, brown hairs 2–3 mm long below, base acute to obtuse, often slightly oblique, apex acuminate (acumen 5–30 mm long), rarely acute, primary vein impressed to flat above, secondary veins distinct, 15–30 on either side of primary vein, flat and often inconspicuous above, more or less forming a marginal vein, at a smallest distance of 1–2 mm from the margin, tertiary veins often inconspicuous, flat above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; pedicels 20–35 mm long, 2–4 mm diam, fruiting pedicels 25–50 mm long, 2–5 mm diam, densely to rather densely covered with erect to appressed, brown hairs, articulated at 0.3–0.5 from the base, bracts 2–4, soon falling, the upper one concave, 15–25 mm long; flower buds broadly ovoid; sepals free, ovate-triangular to broadly ovate-triangular, 4–15(–22) by 5–15(–22) mm, appressed, densely to sparsely covered with appressed, brown hairs; petals green, maturing yellow or purple in vivo, broadly ovate to obovate, 10–20 by 10–15 mm, outer side densely to sparsely covered with appressed, brown hairs 0.5–1.5 mm long; stamens 1–1.5 mm long, connective shield papillate. *Monocarps* 25–65, green, maturing violet to black in vivo, black in sicco, ellipsoid, 8–12 by 4–6 mm, glabrous, apex apiculate (apiculum 0.3–0.5 mm long), wall c. 0.5 mm thick; stipes 3–10 by 1–1.5 mm.



Map 12 Distribution of *Guatteria cuatrecasasii* (●), *G. denudata* (⊙), *G. discolor* (■) and *G. dolichopoda* (□).

Seed ellipsoid, 7–10 by 3–4 mm, dark brown to black, rugose, raphe not distinct from rest of seed.

Distribution — Colombia (Antioquia, Chocó, Riseralda), Ecuador (Esmeraldas).

Habitat & Ecology — In wet, pluvial, or premontane, often secondary forest. At elevations of 80–1500 m. Flowering: April to May; fruiting: August to November.

Vernacular names — Colombia: Cargadero blanco, Cargadero machetico (*D.A. Sánchez S. et al. 885*), Cargadero negro (*Forero et al. 9499*), Cargadero punta de lanza (*D.A. Sánchez S. & Velasquez 878*, *894*, *Hoyos M. & D.A. Sánchez S. 1175*), Cedrillo, Guasco (*Cogollo et al. 2844*), Nuanamú (*D.A. Sánchez S. et al. 307*). Ecuador: Chalviande (*Rubio & Quelal 1323*).

Uses — Colombia: Wood used as firewood and for construction of houses ('La madera se usa como leña y para construcción de viviendas') (*D.A. Sánchez S. & Velasquez 894*, *D.A. Sánchez S. et al. 907*); the bark is used for bags of guasca (fibers) ('la corteza se utiliza para sacar guasca (fibra)'); the bark is used to tie up different tools ('para amarrar o atar diferentes implementos') (*D.A. Sánchez S. et al. 907*). Ecuador: Used for construction ('Usado en construcción') (*Rubio & Quelal 1323*).

Note — *Guatteria cuatrecasasii* may be confused with *G. elegantissima.* For the differences between the species see under the latter.

45. *Guatteria cuscoensis* Maas & Westra, *sp. nov.* — Fig. 31; Map 11

Ab omnibus speciebus peruvianis andicolis pedicellis longioribus differt. — Typus: *Garcia C. et al. 984* (holo WAG; iso CUZ, USM), Peru, Cusco, Paucartambo, Kosñipata, San Pedro, 1650 m, 6 Sept. 2006.

Tree 4–20 m tall, 10–15 cm diam; young twigs rather densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 4–7 mm long, 1–2 mm diam; lamina narrowly elliptic, 9–15 by 3–5 cm (leaf index 2.4–3.5), chartaceous, not verruculose, dull, brown above and below, glabrous above, sparsely covered with appressed hairs below, primary vein rather densely so, base acute to slightly attenuate, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins distinct, 8–12 on either side of primary vein, slightly raised above, smallest distance between loops and margin 2–3 mm, tertiary veins slightly raised above, reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; pedicels 30–60 mm long, 1–1.5 mm diam, fruiting pedicels to c. 2 mm diam, rather densely to sparsely covered with appressed hairs, articulated at 0.1–0.3 from the base, bracts 5–6, soon falling, exceptionally the upper one foliaceous, narrowly elliptic, c. 30 mm long; flower buds depressed ovoid; sepals basally connate or free, broadly ovate-triangular, 3–10 by 4–10 mm, appressed, outer side densely to rather densely covered with appressed hairs; petals pale green, maturing cream, creamy yellow, or beige in vivo, ovate, 15–20 by 8–9 mm, outer side densely covered with appressed, brown hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* 20–40, green, maturing reddish in vivo, brown in sicco, ellipsoid, 10–11 by 5.5–6 mm, glabrous, apex apiculate (apiculum 0.5–1 mm long), wall c. 0.2 mm thick, stipes c. 4 by 1 mm. *Seed* ellipsoid, c. 7 by 4 mm, brown, pitted, raphe not distinct from rest of seed.

Distribution — Peru (Cusco).

Habitat & Ecology — In montane primary or secondary, cloud forest, on rich soil. At elevations of 800–1750 m. Flowering: January, March, June, September; fruiting: July, September, October.

Vernacular names — Not recorded.

Other specimens examined. Peru, **Cusco**, Paucartambo, Kosñipata, San Pedro, 1650 m, 2 Sept. 2006, *Farfán R. et al. 2558* (CUZ, USM, WAG); Paucartambo, Kosñipata, Callanga, 1250 m, 23–30 June 2008, *Farfán R. et al. 4088* (CUZ, USM, WAG); Paucartambo, Kosñipata, San Pedro, 1650 m, 1 Sept. 2006, *Garcia C. et al. 946* (CUZ, USM, WAG); Paucartambo, Kosñipata, San Pedro, 1650 m, 6 Sept. 2006, *Garcia C. et al. 990* (CUZ, USM, WAG); La Convención, Distr. Echarate, Kepashiato, Puguientimari-Pomoreni, 800 m, 24 Mar. 2007, *Valenzuela et al. 9413* (WAG); La Convención, Distr. Echarate, Puyentimari, 831 m, 23 Jan. 2008, *Valenzuela et al. 10766* (WAG); La Convención, Distr. Echarate, Cigakiato, 1000 m, 29 Jan. 2008, *Valenzuela et al. 10962* (WAG).

Note — *Guatteria cuscoensis* occurs in the Peruvian Department of Cusco high in the tropical montane cloud forests of the Manu National Park, and near Kepashiato. It is recognizable from other Andean species of *Guatteria* by its relatively long pedicels and short stipes.

46. *Guatteria darienensis* Susana Arias & Maas — Map 8

Guatteria darienensis Susana Arias & Maas in Arias G. et al. (2014) 150, f. 1. — Type: *Brand & Ascanio 439* (holo HUA; iso JAUM, MO), Colombia, Antioquia, Turbo, Carretera Tapón del Darién, sector Río León-Lomas Aisladas, km 36, 20 m, 27 Aug. 1983.
Guatteria sp. 2 Erkens (2007) 208.

Tree or rarely a shrub 3–16 m tall, 4–18 cm diam; young twigs rather densely to sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2–7 mm long, 1–3 mm diam; lamina narrowly elliptic to narrowly obovate, rarely elliptic, 8–21 by 2.5–8 cm (leaf index 2.5–3.6), chartaceous, not verruculose, dull to shiny, greyish, dark green or brown above, dull, pale brown or brown below, glabrous above, sparsely covered with appressed hairs to almost glabrous below, base acute to attenuate, rarely obtuse, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins distinct, 10–14 on either side of primary vein, impressed to slightly raised above, smallest distance between loops and margin 3–5 mm, tertiary veins inconspicuous or conspicuous, slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 30–75 mm long, c. 1 mm diam, fruiting pedicels 1–1.5 mm diam, rather densely to sparsely covered with appressed and some erect hairs, articulated at 0.2–0.3 from the base, bracts 3–7, soon falling, only one uppermost bract seen, elliptic, c. 7 mm long; flower buds depressed ovoid; sepals basally connate or free, broadly ovate-triangular, 3–7 by 4–6 mm, reflexed, outer side densely covered with appressed hairs; petals green, maturing yellow in vivo, narrowly elliptic, 12–26 by 5–10 mm, outer side densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 35–50, green or pinkish, maturing red to purple in vivo, brown in sicco, ellipsoid or obovoid, 7–10 by 4–5 mm, sparsely covered with appressed hairs, apex apiculate (apiculum c. 0.5 mm long), wall c. 0.1 mm thick, stipes 7–15(–20) by 0.5–1 mm. *Seed* ellipsoid, 6–9 by 3.5–4 mm, shiny, reddish brown, pitted, raphe not distinct from rest of seed.

Distribution — Panama, Colombia (Antioquia, Chocó, Córdoba).

Habitat & Ecology — In lowland or premontane forest, along rivers, creeks, on steep slopes and swampy soils. At elevations of 20–800(–1200) m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Colombia: Guanabanillo (*Zuluaga R. 1226*), Yaya blanca (*D.A. Sánchez S. & Hoyos M. 536*).

Uses — Colombia: Wood is used for building houses and the bark for lashing material and head straps (*D.A. Sánchez S. & Hoyos M. 536*). The decoction of any part of the plant is used against malaria (*Fonnegra et al. 8877*).

Notes — *Guatteria darienensis* is well recognizable by relatively long and slender pedicels (up to 75 mm long in fruit), relatively small monocarps with a very thin wall (c. 0.1 mm thick) and long and slender stipes.

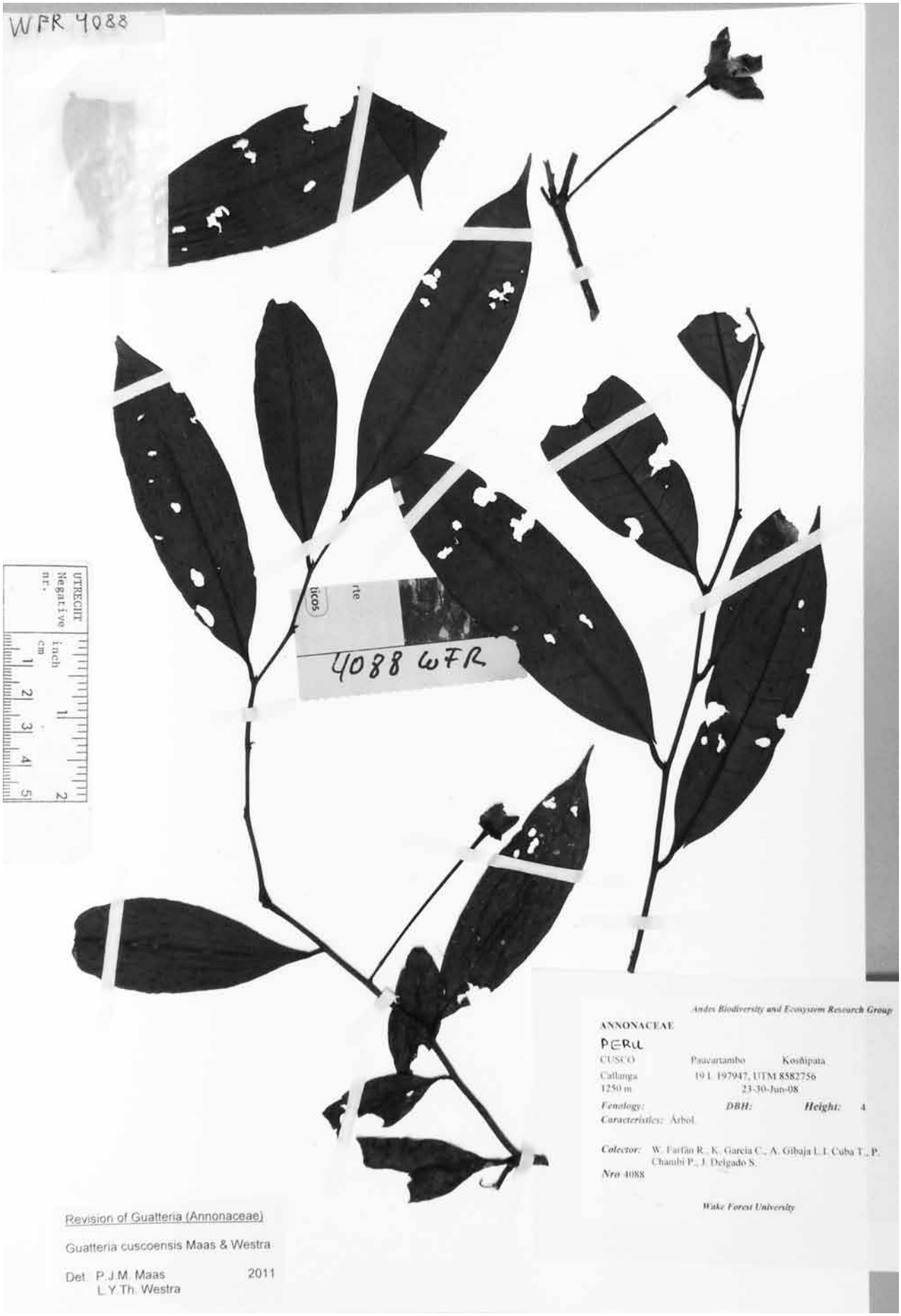


Fig. 31 *Guatteria cuscoensis* Maas & Westra. Flowering branch (*Farfán et al. 4088*, WAG).

Some Panamanian material collected in the province of Panama from ["?]Parque Nacional Altos Campana (*Espinosa et al.720*, *FLORPAN 2962*, *Galdames et al. 3081*, *4136*, *Van der Werff et al. 6198*, *6933*), and one collection from the province of Veraguas (*McPherson 12812*), is aberrant by relatively smaller and thicker leaves (8–12 by 2.5–4.5 cm) with an acute to obtuse base. As all flower, fruit and seed characters match the species concept of *G. darienensis* very well, we refrained from giving this material a status of its own.

47. *Guatteria decurrens* R.E.Fr. — Map 11

Guatteria decurrens R.E.Fr. (1938) 720; Maas & Westra (2011) 119, f. 3c, 5. — Type: *Killip & Smith 29585* (holo US; iso F, NY), Peru, Loreto, Soledad, on Río Itaya, 110 m, 20–22 Sept. 1929.

Guatteria rugosa R.E.Fr. (1939) 501. — Type: *Krukoff 4664* (holo S; iso BM, F, G, K, M, MO, NY, U, US), Brazil, Amazonas, Basin of Rio Juruá, near mouth of Rio Embira, tributary of Rio Tarauacá, 4 June 1933.

Tree 2–35 m tall, 2–60 cm diam; young twigs densely to rather densely covered with rough, brown, erect to half-appressed hairs ('hirsute') to c. 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 pale 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 to c. 2 mm long below, base attenuate to acute, apex acuminate (acumen 10–40 mm long), primary vein impressed above, secondary veins distinct, 13–30 on each side, flat to slightly impressed above, forming a marginal vein, at a smallest distance of 1–5 mm from the margin, tertiary veins inconspicuous and hardly visible above, reticulate. *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 to 2 mm long, articulated at 0.1–0.3 from the base, bracts c. 5, soon falling, not seen; flower buds broadly ovoid to broadly ellipsoid; sepals free or basally connate, ovate-triangular to broadly ovate-triangular, 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 to c. 2 mm long; petals green, yellowish green, maturing yellow or creamy yellow in vivo, elliptic to 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 to 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, longitudinally and transversely grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Colombia (Amazonas), Ecuador (Carchi, Morona-Santiago, Napo, Pastaza, Sucumbios, Zamora-Chinchipe), Peru (Amazonas, Loreto, Pasco), Brazil (Acre, 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) 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*, *Tello 1828*), Espintana (*Ayala et al. 2546*), Yais (Shuar name) (*R. Rojas et al. 36*).

Note — *Guatteria decurrens* can be confused with *G. guianensis*, but it differs by the indument. For further information see under the latter species.

48. *Guatteria delicatula* Maas & Westra, *sp. nov.* — Fig. 24g, 32; Map 11

Frutex parva pro genere, foliis parvis supra conspicue venosis venulis omnino prominentibus monocarpiis in stipitibus articulatis bene distincta. — Typus: *Solomon 9282* (holo U; iso LPB, MO), Bolivia, La Paz, Prov. Nor Yungas, 13.7 km NW of San Pedro on road through Incahuara-Mejillones and along trail to 12 de Octubre, 1500 m, 15–16 Jan. 1983.

Shrub c. 1.5 m tall; young twigs rather densely covered with appressed to semi-erect whitish brown hairs to c. 1 mm long, eventually becoming glabrous. *Leaves*: petiole 2–3 mm long, c. 1 mm diam; lamina narrowly elliptic, 5–7.5 by 1.5–2 cm (leaf index 2.7–3.8), subcoriaceous, not verruculose, dark brown and shiny above, brown and dull below, glabrous above except for rather densely to sparsely hairy primary vein, rather densely covered with appressed to semi-erect hairs to c. 1 mm long on primary vein, elsewhere rather densely to sparsely so below, base acute to obtuse, apex acuminate (acumen 5–10 mm long), primary vein flat to slightly raised above, secondary veins distinct, 10–12 on either side of primary vein, raised above, smallest distance between loops and margin 1–2 mm, tertiary veins raised above, reticulate. *Flowers* solitary in leaf axils, only seen in bud and fruiting stage; fruiting pedicels c. 25 mm long, c. 1 mm diam, rather densely covered with appressed hairs, ultimately glabrous, articulated at c. 0.1 from the base, bracts soon falling, not seen, not countable; flower buds green in vivo, only one loose young bud seen, ovoid, c. 3 by 3 mm, pointed; flowers not seen. *Monocarps* ≤ 20, purplish in vivo, black in sicco, ellipsoid, 5–7 by 4–4.5 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum c. 0.5 mm long), wall c. 0.3 mm thick, stipes 8–10 by 1–1.5 mm, articulated to the monocarp body. *Seed* ellipsoid, c. 6 by 4 mm, brown, transversely grooved, raphe not distinct from rest of seed.

Distribution — Bolivia (La Paz).

Habitat & Ecology — In 'mixture of moist forest with little disturbance and small fields', in secondary growth. At an elevation of c. 1500 m. Flowering: unknown; fruiting: January.

Vernacular names — Not recorded.

Note — *Guatteria delicatula*, only known from the type collection, is one of the smallest (c. 1.5 m tall!) species in the genus, and is recognizable by small leaves with a distinctly raised venation on the upper side and by the stipes which are articulate to the monocarp body. The articulation is clearly visible as a constriction between the stipes and the monocarp body. This is not often seen in the genus as a whole.

49. *Guatteria denudata* R.E.Fr. — Map 12

Guatteria denudata R.E.Fr. (1957b) 601; Maas & Westra (2010) 264, f. 6. — Type: *Schultes & Cabrera R. 17374* (holo S; iso COAH, GH, NY, US), Colombia, Vaupés, Río Piraparaná, tributary of Río Apaporis, headwaters of Caño Teemeeña, 10 Sept. 1952.

Tree small (1.5 m) to medium-sized, diam not recorded; young twigs sparsely covered with appressed hairs or very soon glabrous. *Leaves*: petiole 5–15 mm long, 1–2 mm diam; lamina elliptic to narrowly elliptic, or narrowly oblong-elliptic, 7–15 by 3–6 cm (leaf index 1.7–2.8), coriaceous, not verruculose, shiny and dark brown above, brown below, glabrous above and below, base obtuse, extreme base slightly attenuate, apex acuminate (acumen 10–20 mm long), primary vein impressed above, secondary veins indistinct, 12–15 on either side of primary vein (hardly countable), slightly raised above, smallest

Fig. 32 *Guatteria delicatula* Maas & Westra. Flowering and fruiting branch (*Solomon 9282*, holotype U).

distance between loops and margin 2–5 mm, tertiary veins flat to slightly raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 6–22 mm long, 1–1.5 mm diam, fruiting pedicels to c. 2 mm diam, articulated at 0.1–0.2 from the base, rather densely covered with appressed, brownish hairs to glabrous, bracts 4–5, soon falling, not seen; flower buds not seen; sepals free, broadly ovate-triangular, 3–4 by 4–6 mm, appressed, outer side sparsely covered with appressed hairs; petals green in vivo, narrowly oblong-elliptic to oblong-elliptic, 10–22 by 4–13 mm, outer base densely covered with appressed hairs, otherwise sparsely so; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 25–30, colour in vivo not recorded, dark brown to brown in sicco, ellipsoid, 8–9 by 3–4 mm, glabrous, apex rounded, wall c. 0.2 mm thick, stipes 2–3 by 1–1.5 mm. *Seed* ellipsoid, 8–9 by 4 mm, brown, rugose to pitted, raphe not distinct from rest of seed.

Distribution — Amazonian Colombia (Vaupés).

Habitat & Ecology — Vegetation type not recorded. At about sea level. Flowering: September; fruiting: September.

Vernacular name — Colombia: Feé-ka-no (Baras name) (*Schultes & Cabrera R. 17374*).

Note — *Guatteria denudata* (included by R.E. Fries in sect. *Pteropus*) is a poorly known species from 2 gatherings only. It is quite noteworthy by its very thick, shiny, glabrous leaves with an obtuse base, the extreme base being slightly attenuate.

50. *Guatteria discolor* R.E.Fr. — Map 12

Guatteria discolor R.E.Fr. (1939) 509, f. 33a; Maas et al. (2007) 638; Erkens et al. (2008) 483, pl. 2. — Type: *Krukoff 7047* (holo S; iso B, BR, F 2 sheets, G, K, MO, NY, U, US 2 sheets), Brazil, Amazonas, Basin of Rio Madeira, Mun. Humaitá, on plateau between Rio Livramento and Rio Ipixuna, 7–18 Nov. 1934.

Tree 13–30 m tall, 25–80 cm diam, often with plank buttresses; young twigs densely to rather densely covered with erect, reddish brown, curly hairs, soon glabrous. *Leaves*: petiole 5–10(–15) mm long, 2–4 mm diam; lamina narrowly elliptic, 15–30 by 4–10 cm (leaf index 2.8–3.7), coriaceous, sparsely to densely verruculose or not verruculose, dull, grey to greyish black above, dark brown below, rather densely covered with erect and appressed, brown hairs above, soon glabrous, densely covered with erect, reddish brown, curly hairs below, base acute, extreme base attenuate, shortly decurrent along petiole, apex acute to acuminate (acumen 10–15 mm long), primary vein impressed to raised above, secondary veins distinct, 15–25 on either side of primary vein, impressed above, smallest distance between loops and margin 1–2 mm, tertiary veins flat to slightly raised above, reticulate to percurrent. *Flowers* in 1–3-flowered inflorescences in axils of leaves; pedicels 10–20 mm long, 1–2 mm diam, fruiting pedicels to c. 25 mm long, 3–5 mm diam, densely covered with erect, reddish brown, curly hairs, articulated at 0.3–0.5 from the base, bracts 5–6, soon falling, broadly elliptic to elliptic, basal bracts 1–2 mm long, upper ones 8–11 mm; flower buds ovoid, pointed; sepals free, broadly ovate-triangular to ovate-triangular, 6–13 by 5–6 mm, spreading to reflexed, outer side densely covered with erect, reddish brown, curly hairs; petals green, maturing yellowish in vivo, narrowly ovate to narrowly obovate, 15–40 by 6–16 mm, outer side densely covered with erect, reddish brown, curly hairs; stamens c. 2 mm long, connective shield papillate, umbonate or not. *Monocarps* 10–30, dark green, maturing blueish black to black in vivo, dark brown to black in sicco, ellipsoid to narrowly so, 15–30 by 7–15 mm, surface irregularly wrinkled in sicco, sparsely covered with erect, reddish brown, curly hairs, apex rounded to apiculate (apiculum < 0.5 mm long), wall 0.5–1 mm thick, stipes 2–10 by 1–2 mm. *Seed* narrowly ellipsoid to ellipsoid, 13–17 by 6–9 mm, brown, smooth, raphe not distinct from rest of seed.

Distribution — Colombia (Amazonas, Vaupés), French Guiana, Amazonian Peru (Loreto, Madre de Dios), Brazil (Acre, Amazonas, Rondônia), Bolivia (La Paz, Pando).

Habitat & Ecology — In non-inundated forest, sometimes in campinarana vegetation (Brazil, Acre), on clayey, sometimes on sandy soil. At elevations of 0–600 m. Flowering: October to January, April; fruiting: January, April to July, October, November.

Vernacular names — Bolivia: Piraquina blanca (*Terceros 1398*). Brazil: Envira (*Krukoff 7047*, *Unknown collector 17*, *21*), Envira-bobo (*Boom et al. 8635*), Envira-fofa, Envira-mole-da-folha-grande (*Daly et al. 7794*), Envira-preta, Envira-rolinha, Envireira (*Daly et al. 7037*). French Guiana: Matau'i, (Wayãpi name) (*Grenand 554*), Miret (Palikur name).

Notes — *Guatteria discolor* can be distinguished fairly easily by its 2-coloured leaves which are covered with an indument of erect, reddish brown, curly hairs on the lower side. Furthermore, the monocarps are fairly large and wrinkled when dry, the latter feature not often seen in the genus. A third remarkable aspect are the distinctly pointed flower buds. See also under *G. chrysophylla*.

Guatteria discolor was placed by Fries (1939: 509) into a section of its own, namely sect. *Dichrophyllum*, characterized by 2-coloured leaves, a persistent indument of brownish hairs, and by leaves which are verruculose on the upper side. The latter feature appears to be quite variable, the density of verruculae ranging from densely to sparsely, and we even noticed leaves without any warts.

A vegetative collection from Bolivia (*Chatrou et al. 438* (MO, U)) has very large leaves measuring 40 by 15 cm!

51. *Guatteria dolichopoda* Donn.Sm. — Plate 3e; Map 12

Guatteria dolichopoda Donn.Sm. (1897) 2; R.E.Fr. (1939) 357. — Type: *Donnell Smith 6429* (lecto US, selected by Erkens 2007; isolecto B, C, G, GH, K 2 sheets, M, MO, US), Costa Rica, San José, La Concepción, Llanuras de Santa Clara, 250 m, Feb. 1896.

Guatteria tonduzii Diels [var. *tonduzii*] (1931) 75; R.E.Fr. (1939) 356. — Type: *Tonduz 17680* (holo B; iso BM, F, G 3 sheets, K, US 2 sheets, Z), Costa Rica, Heredia, 'Collines de Tremedal, près San Ramon', 1300–1400 m, 10 Apr. 1913.

Guatteria tonduzii Diels var. *leptopus* R.E.Fr. (1939) 357. — Type: *Pittier 10958* (holo M; iso BR 2 sheets, C, G 3 sheets, US), Costa Rica, Puntarenas, Cañas Gordas, 1100 m, Mar. 1897.

Guatteria dolichopoda Donn.Sm. var. *microsperma* R.E.Fr. (1939) 358, f. 8a. — Type: *Tonduz 9166* (holo S; iso BM, BR 3 sheets, C, K 2 sheets, M, P, S, US 7 sheets, W), Costa Rica, Limón, Shiroles ('Forêts a Shirores, Talamanca'), 100 m, Feb. 1895.

Guatteria rigidipes R.E.Fr. (1939) 358, t. 21. — Type: *Skutch 2553* (holo S; iso K, MO, NY, US), Costa Rica, San José, vicinity of El General, 1040 m, Feb. 1936.

Tree or shrub 3–20 m tall, 10–20(–100) cm diam; rather densely to sparsely covered with erect, brown hairs c. 0.5 mm long, finally glabrous. *Leaves*: petiole 2–6 mm long, 1 mm diam; lamina narrowly elliptic, sometimes narrowly ovate, 11–14 by 2–5 cm (leaf index 2.8–5.5), chartaceous, not verruculose, dull, greyish black to greyish brown above, greyish to brown below, glabrous above, but primary vein and sometimes the secondary veins covered with erect, brown hairs, sparsely covered with erect (and appressed), brown hairs below, base acute to attenuate, apex acuminate (acumen 10–20 mm long), primary vein impressed to flat above, secondary veins indistinct, 10–15 on either side of primary vein, flat to slightly raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; flowering and fruiting pedicels

Fig. 33 *Guatteria dotana* N. Zamora & Erkens. Fruiting branch (*Estrada & Valverde 1084*, isotype MO).

30–60 mm long, c. 1 mm diam, rather densely to sparsely covered with erect hairs, becoming almost glabrous in fruit, articulated at 0.1–0.2 from the base, bracts 4–6, soon falling, rarely present, uppermost bract narrowly elliptic, to c. 8 mm long; flower buds depressed ovoid, slightly pointed; sepals free, ovate-triangular to broadly ovate-triangular, 5–7 by 3–6 mm, reflexed, outer margins revolute, outer side rather densely to sparsely covered with appressed hairs; petals green, maturing yellow in vivo, narrowly oblong-elliptic to narrowly ovate, 14–30 by 4–11 mm, outer side densely to rather densely covered with appressed, white hairs, particularly towards the base; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 75–100, black in vivo, black in sicco, ellipsoid, 7–11 by 4–5 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 1 mm long), wall 0.1–0.2 mm thick, stipes 15–20 by 1 mm. *Seed* ellipsoid, 6–9 by 4–5 mm, dark brown, pitted, raphe raised.

Distribution — Honduras, Costa Rica, Panama.

Habitat & Ecology — In lowland or lower montane forest. At elevations of 0–1600 m. Flowering: January to July; fruiting: December to July.

Vernacular names — Not recorded.

Note — *Guatteria dolichopoda* is recognized by its quite long pedicels and young twigs covered with erect hairs c. 0.5 mm long. It has often been confused with *G. tomentosa*, see under that species for a discussion.

52. *Guatteria dotana* N.Zamora & Erkens, *sp. nov*. — Fig. 24h, 33; Map 11

Ramulis novellis plusminusve fractiflexis pilis appressis dense obtectis, floribus breviter pedicellatis monocarpiis breviter stipitatis facile recognoscenda. — Typus: *Estrada & Valverde 1084* (holo CR; iso MO), Costa Rica, San José, Tarrazu, Llanos de Santa María de Dota, Cerro Nene, Finca de Henry Marín, 900–1300 m, 19 Aug. 1997.

Tree 4–7 m tall, diam not recorded; young twigs densely to rather densely covered with brown, appressed hairs, slightly zigzagging. *Leaves*: petiole 5–8 mm long, c. 2 mm diam; lamina narrowly oblong-elliptic, 10–21 by 3–8 cm (leaf index 2.6–3.3), coriaceous, not verruculose, shiny to dull, greyish green above, pale brown below, glabrous above, densely to sparsely covered with appressed, reddish hairs mainly along the primary vein below, base acute to obtuse, apex acuminate (acumen 5–15 mm long), primary vein flat to slightly raised above, secondary veins distinct, 11–17 on either side of primary vein, slightly raised above, smallest distance between loops and margin 2–3 mm, tertiary veins slightly raised above, reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; pedicels 0–7 mm long, c. 1 mm diam, fruiting pedicels 5–15 mm long, 2–4 mm diam, densely covered with appressed, pale brown hairs, articulated at 0.3–0.5 from the base, bracts 5–6, soon falling, not seen; flower buds ovoid; sepals free, broadly ovate-triangular, 6–8 by 5–7 mm, reflexed, outer side densely covered with appressed hairs; petals greenish to cream in vivo, ovate-elliptic, 7–12(–14) by 6–8 mm, outer side densely covered with appressed hairs; stamens c. 2 mm long, connective shield hairy. *Monocarps* 15–25, green, maturing purplish black in vivo, black in sicco, ellipsoid, 15–17 by 6–10 mm, glabrous, apex rounded, wall 0.1–0.2 mm thick, stipes 4–6 by 1 mm. *Seed* ellipsoid, 12–14 by 6–7 mm, dark, shiny brown, transversely grooved (to pitted), raphe raised.

Distribution — Costa Rica.

Habitat & Ecology — Wet forest ('bosque muy húmedo'). At elevations of 500–1300 m. Flowering: February, May; fruiting: August, October.

Vernacular names — Not recorded.

Other specimens examined. Costa Rica, **Puntarenas**, Buenos Aires, Colinas, Fila Retinto, parte alta de la Fila, 1017 m, 22 May 2012 (fl), *Lobo 3343* (CR). **San José**, Dota, San Isidro, Cerro Tijerilla, 900–1000 m, 21 Oct. 1998 (fr), *Estrada & Solano 1817* (CR, MO); Tarrazú, ZP Cerro Nara, Cuenca del Naranjoy Paquita, Dota, 2 km del cruce à Río Blanco, camino a San Isidro, 300–600 m, 27 Feb. 2005, *Santamaría & Morales 682* (CR, L); Dota, Reserva Forestal Los Santos, Cuenca del Savegre, Quebrada Bomba, cruce a Fila Mona y La Bomba, 500 m, 28 Feb. 2005 (fl), *Santamaría & Morales 757* (INB); Dota, Reserva Forestal Los Santos, Cuenca del Savegre, San Isidro de Dota, albergue Timaná, 800–900 m, 1 Mar. 2005, *Santamaría & Morales 809* (CR, L).

Note — *Guatteria dotana*, endemic to Costa Rica, can be distinguished by zigzagging young twigs which are densely covered with appressed, brownish to reddish hairs, very shortly pedicellate flowers and shortly stipitate monocarps.

53. *Guatteria duckeana* R.E.Fr. — Fig. 34; Map 13

Guatteria duckeana R.E.Fr. (1939) 468, f. 22f, g. — Type: *Ducke RB 29019* (holo S; iso RB), Brazil, Amazonas, Manaus, Ponte do Mindu ('loco Ponte de Mindú, ad ripam rivuli'), Nov. 1935.

Tree 6–15 m tall, c. 7.5 cm diam; young twigs densely to rather densely covered with erect hairs, soon glabrous. *Leaves*: petiole 3–10 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly ovate, 10–22 by 4–6 cm (leaf index 2.5–4), coriaceous, not verruculose, shiny, dark brown above, brown below, rather densely to sparsely covered with erect hairs above, soon glabrous, densely to rather densely covered with erect hairs below (hairs simple, intermixed or not with few bundles of 2 hairs), base acute, obtuse, or attenuate, basal margins mostly revolute, apex acuminate (acumen 5–15 mm long), primary vein flat above, secondary veins indistinct, 8–15 on either side of primary vein, flat above, smallest distance between loops and margin 2–4(–8) mm, tertiary veins flat above, reticulate. *Flowers* in 1–3-flowered inflorescences in axils of leaves; flowering and fruiting pedicels 5–8 mm long, 1–2 mm diam, densely covered with erect hairs, soon becoming subglabrous, articulated at 0.3–0.6 from the base, bracts c. 5, soon falling, one basal bract seen, broadly elliptic, c. 2 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–5 by 3–5 mm, reflexed, outer side densely covered with appressed hairs, margins revolute; petals green when young in vivo, oblong-elliptic, 8–20 by 5–8 mm, outer side densely covered with erect hairs, soon becoming subglabrous, margins revolute; stamens 1–1.5 mm long, connective shield densely hairy. *Monocarps* 10–20, green in vivo, brown in sicco, ellipsoid to fusiform, 9–18 by 6–10 mm, longitudinally wrinkled in sicco, sparsely covered with erect hairs, soon becoming glabrous, apex rounded to apiculate (apiculum to. 1 mm long), wall c. 1 mm thick, stipes 0–4 by 2 mm. *Seed* ellipsoid, c. 15 by 7 mm, pale brown, smooth, raphe not distinct from rest of seed.

Distribution — Brazil (Amazonas, Manaus Region).

Habitat & Ecology — In non-inundated, primary or secondary terra firme forest, one collection from campinarana vegetation, on sandy soil. At elevations of about sea level. Flowering: January, October; fruiting: January, August to October.

Vernacular names — Brazil: Envira (*Krukoff 7923*), Envireira (*L. Coêlho INPA 5805*).

Notes — *Guatteria duckeana* together with *G. citriodora*, *G. schomburgkiana* and *G. stipitata* forms part of the *G. schomburgkiana* complex, see Table 4 (p. 59). This group, placed by Fries (1939) in sect. *Cephalocarpus* which originally consisted of eight species, has as its main features short-pedicelled flowers and sessile to very shortly stipitate monocarps. The densely hairy connective shield also is a distinctive feature of this group (vs papillate or glabrous in most *Guatteria* species).

Fig. 34 *Guatteria duckeana* R.E.Fr. Flowering branch (*Ducke RB 29019*, holotype S).

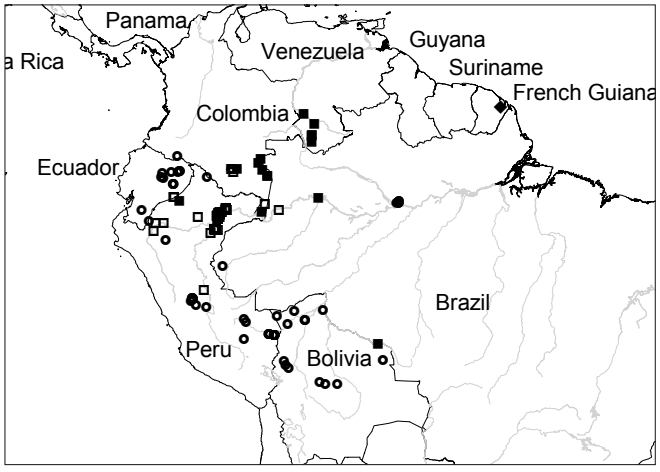
Guatteria duckeana, restricted to the Manaus region in Central Amazonian Brazil, is marked by coriaceous leaves with indistinct venation and revolute margins near the base, sepals and petals with revolute margins, and by its very large, subsessile monocarps and pointed seeds of c. 15 by 7 mm.

54. *Guatteria duodecima* Maas & Westra — Map 13

Guatteria duodecima Maas & Westra in Erkens et al. (2008) 483, f. 6; Maas & Westra (2011) 121. — 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 c. 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, tertiary veins raised above, reticulate. *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 to c. 25 mm long, 2–3 mm diam, densely covered with appressed hairs, articulated at 0.2–0.6 from the base, bracts 3–5, soon falling, the upper one 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, maturing brownish yellow in vivo, 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 to 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, rugose, raphe raised.

Distribution — Amazonian Ecuador (Morona-Santiago, Napo, Pastaza, Zamora-Chinchipe), Peru (Cusco, Loreto, Madre de Dios, Pasco, San Martín), Brazil (Acre), Bolivia (Beni, La Paz, Pando, Santa Cruz).



Map 13 Distribution of *Guatteria duckeana* (●), *G. duodecima* (⭘), *G. dura* (■), *G. elata* (□) and *G. elegans* (◆).

Habitat & Ecology — In non-inundated, lowland rain forest to premontane forest, sometimes in periodically inundated forest. At elevations of 150–1800 m. Flowering: throughout the year; fruiting: May to November.

Vernacular names — Bolivia: Oyshobo (Yuracare name) (*Thomas & Agustin 2024*), Piraquina (*Thomas & Agustin 2024*). Peru: Atzmiriqui (*D.N. Smith 5290*).

Field observations — Flowers of *G. duodecima* reportedly have an apple-like odor (*Korning & Thomsen 47656*).

Notes — *Guatteria duodecima* at first glance can be distinguished by relatively narrow and verruculose leaves, usually narrowed towards both ends, and which are densely to rather densely covered with appressed, almost silvery hairs on the lower side. Other distinctive features are the shortly pedicellate flowers, and monocarps that are always longer that the stipes.

The lower side of the leaves is mentioned as having a silvery shine (*Chatrou et al. 25*).

55. *Guatteria dura* R.E.Fr. — Map 13

Guatteria dura R.E.Fr. (1939) 499; Maas & Westra (2011) 121, f. 1b, 6, 7. — Type: *Spruce 3354* (holo K; iso BM, BR, K, P), Venezuela, Amazonas, Río Pasimoni, Feb. 1852.
Guatteria kuhlmannii R.E.Fr. (1939) 498. — Type: *J.G. Kuhlmann 460 = RB 24256* (holo S; iso NY, RB, SPF), Brazil, Rondônia, Rio Ouro Preto, affluent of Rio Pacaás Novos, 17 Sept. 1923.

Tree or shrub 2–30 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, often slightly attenuate, apex 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 distance between loops and margin 2–5 mm, tertiary veins inconspicuous and hardly visible above, percurrent to reticulate. *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 to c. 30 mm long, c. 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 uppermost broadly ovate, c. 4 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 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 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 to longitudinally grooved, raphe not distinct from rest of seed.

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

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

Fig. 35 *Guatteria elata* R.E.Fr. Fruiting branch (*T.D. Pennington et al. 17006*, U).

Vernacular names — Colombia: Jaacu (Muinane name), Jaacuo (Muinane name) (V*an Andel et al. 136*), Jakup (Muinane name) (*Urrego et al. 1417*, *1572*), Jimogï (Huitoto name) (*Urrego et al. 1785*, *1979*), Vara blanca (*Urrego et al. 293A*). Peru: Carahuasca (*Rimachi Y. 8814*). Venezuela: Majagua (*Ll. Williams 15862*), Majagua negra (*Velazco 2007*).

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

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 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.

56. *Guatteria elata* R.E.Fr. — Fig. 35, 36a; Map 13

Guatteria elata R.E.Fr. (1938) 712; (1939) 499; Spichiger in Spichiger et al. (1989) 121, f. 56; Murillo A. & Restrepo (2000) 92, f. 24. — Type: *Krukoff 8356* (holo S; iso A, BM, BR, F, G, K, MO, P, U, US 2 sheets), Brazil, Amazonas, Basin of Rio Solimões, Mun. São Paulo de Olivença, near Palmares, 11 Sept. to 26 Oct. 1936.

Tree or shrub 7–35 m tall, 15–45 cm diam; young twigs densely to sparsely covered with appressed hairs 0.2–2 mm long, soon glabrous. *Leaves*: petiole 5–10 mm long, 1–1.5 mm diam; lamina narrowly elliptic, rarely narrowly obovate, 8–17 by 2–5 cm (leaf index 2.8–4), coriaceous, not verruculose, dull above, dark brown to blackish brown above, brown to dark brown below, glabrous above, rather densely to sparsely covered with appressed hairs 0.5–1 mm long below, base attenuate, apex acuminate (acumen 5–20 mm long), primary vein impressed above, rounded to distinctly keeled below, secondary veins indistinct, 10–15 on either side of primary vein, slightly raised above, smallest distance between loops and margin 2–5 mm, tertiary veins inconspicuous, flat above, reticulate to percurrent. *Flowers* in 1(–3)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–25 mm long, c. 1 mm diam, fruiting pedicels to c. 3 mm diam, rather densely covered with appressed hairs, articulated at 0.2–0.4 from the base, bracts 5–6, soon falling (only scars seen); flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–6 by 5–6 mm, reflexed, outer side densely covered with appressed, greyish hairs; petals green, maturing cream or yellow in vivo, narrowly elliptic to elliptic or obovate, 20–25 by 5–12 mm, outer side densely covered with appressed hairs, particularly the base; stamens 1–1.5 mm long, connective shield papillate, umbonate or not. *Monocarps* 30–75, green, maturing black in vivo, black to brown in sicco, ellipsoid, 10–12 by 5–6 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum 0.1–0.5 mm long), wall 0.2–0.3 mm thick, stipes 15–25 by c. 1 mm. *Seed* ellipsoid, 8–11 by 4–6 mm, dark, shiny brown, pitted, raphe raised.

Distribution — Amazonian Colombia (Amazonas, Vaupés), Brazil (Amazonas), Peru (Loreto).

Habitat & Ecology — In non-inundated forest, on sandy to sandy-clayey soil. At elevations of up to 200 m. Flowering: July to March; fruiting: March, August to October, December.

Vernacular names — Peru: Carahuasca (*Daly et al. 5797*, *Daza 26*, *Valcarcel 399-2G*, *Vásquez et al. 7124*, *9364*), Carahuasca negra (*J. Ruiz 1074*), Espintana (*Spichiger et al. 1770*).

Notes — *Guatteria elata* is recognizable by its brownish (in sicco!) lamina, an indistinct secondary leaf venation, an attenuate leaf base and an inconspicuous indument of appressed hairs on the lower side of the lamina.

A diameter of 15 feet is mentioned on the type label, which seems highly unlikely. Other label annotations we came across did not give bigger diameters than 45 cm.

One of the two Colombian collections, namely *Zarucchi 1924* (U) from Mitú, Vaupés, probably belongs here, although it is aberrant in having relatively short stipes (5–15 mm vs 15–25 mm in normal *G. elata*).

57. *Guatteria elegans* Scharf — Map 13

Guatteria elegans Scharf in Scharf et al. (2006a) 121, f. 2. — Type: *Feuillet et al. 10256* (holo NY; iso BBS, K, M, U 2 sheets), French Guiana, Régina, Mt Tortue, 11 km WNW of the Approuague River, along road direction of Cayenne, 200–450 m, 18 June 1988.

Treelet c. 4 m tall, diam not recorded; young twigs sparsely to densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 3–5 mm long, c. 1 mm diam; lamina narrowly elliptic, 10–16 by 3–4 cm (leaf index 2.7–4), chartaceous to subcoriaceous, not verruculose, dark brown above, brown below, glabrous above, except for sparsely hairy primary vein when young, sparsely covered with appressed hairs below, base acute, apex acuminate (acumen 15–25 mm long), primary vein slightly impressed to flat above, secondary veins distinct, 5–8 on either side of primary vein, impressed above, angle of secondary vein with primary vein 30–40°, smallest distance between loops and margin 2–3 mm, tertiary veins slightly raised above, percurrent to reticulate. *Flowers* solitary on leafless branchlets; fruiting pedicels 20–25 mm long, 1–1.5 mm diam, sparsely covered with appressed hairs, soon glabrous, articulated at c. 0.2 from the base, bracts 5–6, soon falling, not seen; flower buds not seen; sepals free, shallowly ovate-triangular, c. 2 by 3 mm, apically reflexed, glabrous; petals and stamens not seen. *Monocarps* 10–25, green in vivo, blackish brown in sicco, ellipsoid, 7–8 by 4–5 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum 0.5–1 mm long), wall 0.1–0.2 mm thick, stipes 11–15 by c. 0.5 mm. *Seed* ellipsoid, 6–7 by c. 4 mm, pale brown, pitted to transversely grooved, raphe not distinct from rest of seed.

Distribution — French Guiana.

Habitat & Ecology — In low, non-inundated ('montane') rain forest, on lateritic soil. At elevations of 200–450 m. Flowering: unknown; fruiting: June.

Vernacular names — Not recorded.

Note — *Guatteria elegans*, only known from the type collection, is recognizable by the low number of secondary veins (5–8) for the genus. A sharp angle of 30–40° between primary vein and secondaries is not occurring in any other *Guatteria* species in the Guianas and Brazilian Amazonia.

58. *Guatteria elegantissima* R.E.Fr. — Fig. 37; Map 14

Guatteria elegantissima R.E.Fr. (1950a) 338, pl. 4. — Type: *Cuatrecasas 17305* (holo S; iso COL 2 sheets, F 2 sheets, L, U, US), Colombia, Valle del Cauca, Costa del Pacífico, Río Cajambre, San Isidro, 5–100 m, 2–5 May 1944.

Tree 5–25 m tall, 5–80 cm diam; young twigs somewhat zigzagging, densely covered with long-persisting, erect, brown hairs. *Leaves*: petiole 1–3 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly ovate, 7–22 by 2–3.5 cm (leaf

Fig. 36 a. *Guatteria elata* R.E.Fr. Flower. – b. *Guatteria fractiflexa* Maas & Westra. Flower. – c. *Guatteria herrerana* N.Zamora & Maas. Fruit on stem. – d, e. *Guatteria hirsuta* Ruiz & Pav. d. Flowers; e. fruit. – f, g. *Guatteria maguirei* R.E.Fr. f. Flowers; g. fruit. – h. *Guatteria maypurensis* Kunth. Fruit (a: *Daly et al. 5797*, U; b: *Vásquez 27596*, U; c: *G. Herrera C. 8401*, holotype part CR; d: *Killeen 2802*, U; e: *W. Palacios 7526*, U; f: *O. Huber 5130*, U; g: *Huber & Tillett 2888*, U; h: *Zarucchi & Barbosa 3828*, U).

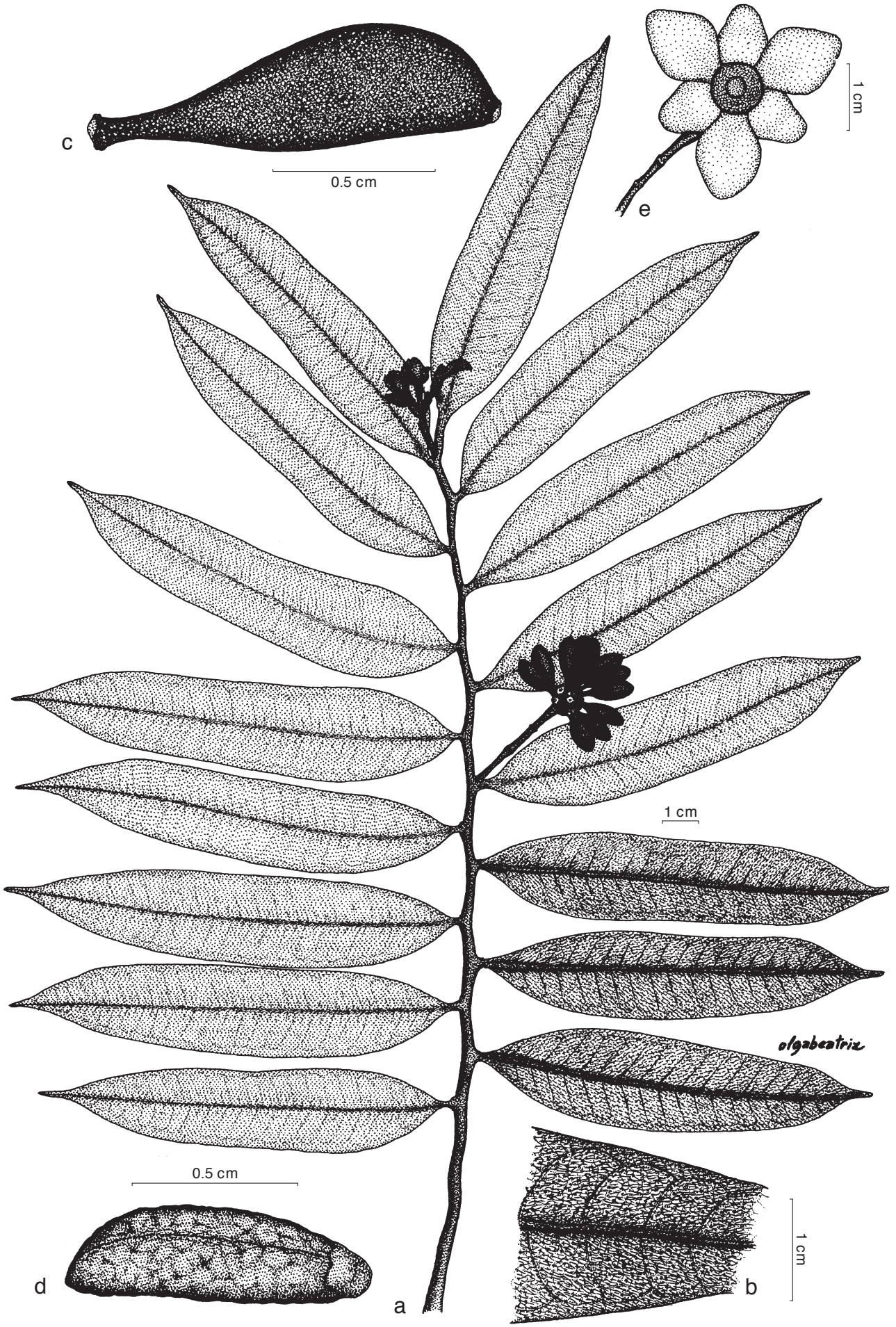


Fig. 37 *Guatteria elegantissima* R.E.Fr. a. Fruiting branch; b. detail of indument of lamina; c. loose monocarp; d. seed; e. flower (a–d: *Cuatrecasas 17305*, isotype COL; e: *D.A. Sánchez S. 785*, MEDEL; from Sánchez S. (1986) f. 20).

index 3.8–5.8), chartaceous, densely verruculose, dull, dark brown or dark green above, paler brown or green below, glabrous above, but the primary vein densely covered with erect, brown hairs, densely covered with erect, brown hairs below, base acute, rarely obtuse, apex acuminate (acumen 5–20 mm long), primary vein impressed above, secondary veins indistinct to distinct, 12–20 on either side of primary vein, flat to slightly impressed above, more or less forming a marginal vein, at a smallest distance of 1–3 mm fom the margin, tertiary veins inconspicuous, flat to slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 20–40 mm long, 1–1.5 mm diam, fruiting pedicels to c. 3 mm diam, rather densely to densely covered with erect, brown hairs, articulated at c. 0.3 from the base, bracts 3–6, soon falling, the basal ones 10–14 mm long, the 2 upper ones 13–16 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 5–7 by 5–6 mm, appressed, outer side sparsely covered with appressed, brown hairs; petals green or yellow in vivo, broadly ovate to ovate, 9–13 by 7–10 mm, outer side densely covered with erect, brown hairs to almost glabrous, except for the hairy margins; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* 40–50, dark green, maturing black in vivo, blackish in sicco, narrowly ellipsoid to ellipsoid, 5–8 by 2–4 mm, glabrous, except for a few scattered, appressed hairs, apex acute to apiculate (apiculum 0.1–0.2 mm long), wall 0.1–0.5 mm thick, stipes 2–5 by c. 1 mm. *Seed* narrowly ellipsoid, 6–8 by 2–4 mm, dull, dark brown, rugulose, raphe not distinct from rest of seed.

Distribution — Pacific coast of Colombia (Valle del Cauca).

Habitat & Ecology — In wet, tropical rain forest, along the margin of rivers and along roads, on loamy to clayey soil. At elevations of 0–350 m. Flowering: February to August; fruiting: February, April, May, July, August, October.

Vernacular names — Colombia: Cargadero (*Gentry et al. 48326*), Cargadero negro (*D.A. Sánchez S. 676*).

Notes — *Guatteria elegantissima* can very easily be recognized by the very densely verruculose and shortly petiolate leaves which are densely covered with erect, brown hairs on the lower side. Moreover, the monocarps are quite characteristic in often being narrowly ellipsoid and shortly stipitate. *Guatteria elegantissima* looks somewhat similar to *G. cuatrecasasii*, differing by smaller leaves and a less dense indument of shorter hairs than in *G. cuatrecasasii.*

Wisum et al. 24 (MO) from Ecuador, Morona-Santiago occurs at quite some distance from Valle del Cauca in Colombia were all other gatherings were done. It is also remarkable because it occurs at an elevation of > 1200 m while in Colombia collections were found at elevations below 400 m. Apart from this it matches well the other material albeit with slightly larger monocarps.

59. *Guatteria elongata* Benth. — Map 14

Guatteria elongata Benth. (1843) 359; R.E.Fr. (1939) 431, t. 30. — Type: *R.H. Schomburgk I 962* (holo K; iso B, BM, E, F, G, K, L, P, U, US, W), Brazil, Rio Negro, without further exact location, anno 1839.

Tree of unknown height and diam; young twigs densely covered with appressed, brown hairs to c. 1 mm long, soon glabrous. *Leaves*: petiole 5–15 mm long, 1–2 mm diam; lamina narrowly oblong-elliptic, 12–23 by 5–6.5 cm (leaf index 3.8–5), chartaceous, not verruculose, shiny above, brown on both sides, glabrous above, sparsely covered with appressed, brown hairs to c. 1 mm long below, base acute, extreme base attenuate, apex acute to acuminate (acumen to c. 10 mm long), primary vein impressed above, secondary veins distinct, 12–15 on either side of primary vein, slightly raised above, smallest distance between loops and margin 3–4 mm, tertiary veins inconspicuous, slightly raised above, reticulate. *Flowers* in (1–)2–4-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 2–8 mm long, 1.5–2 mm diam, densely covered with appressed, brown hairs to c. 1 mm long, articulated at 0.5–0.6 from the base, bracts c. 6, soon falling, basal bract (one seen) very broadly ovate, c. 1 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–5 by 5–6 mm, appressed, outer side densely covered with appressed, brown hairs to c. 1 mm long; petals colour not recorded, obovate, 12–18 by 6–8 mm, outer side densely covered with appressed, brown hairs to c. 1 mm long at the base, towards the apex the hairs whitish; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* and *seed* not seen.

Distribution — Amazonian Brazil (Amazonas).

Habitat & Ecology — Vegetation type not recorded. At an elevation of about sea level. Flowering: unknown; fruiting: unknown.

Vernacular names — Not recorded.

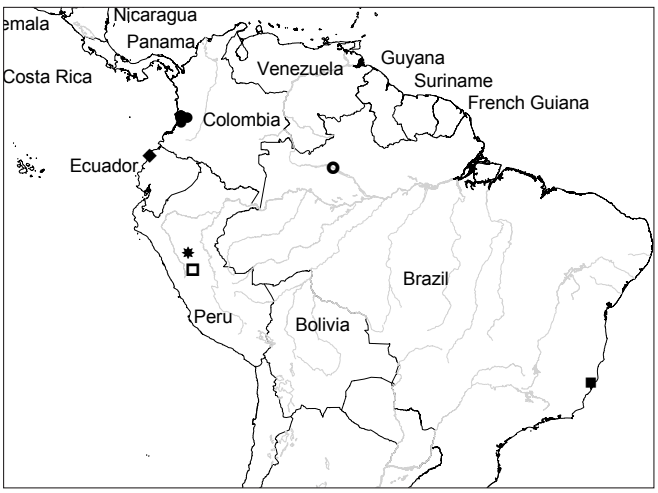
Notes — *Guatteria elongata* was placed by Fries (1939) into a section of its own, sect. *Pycnantha* (= 'flowers crowded together'), because of its many-flowered inflorescences and very short pedicels. As the species has never been collected since and as the material available is incomplete we cannot place it yet anywhere in the genus. It shows superficially some features of *G. subsessilis* (the short pedicels) but from that species it differs by a completely different indument (long, brown, appressed hairs in leaves, flowers, pedicels, sepals, etc. in *G. elongata* vs almost completely glabrous in all parts of *G. subsessilis*).

Several collections of this species have been labelled as 'British Guiana', but according to Van Dam (2002: 88, 89) the Robert Schomburgk type collection comes from the Rio Negro in Amazonian Brazil. The exact location could not be traced, but it is probably situated between Barcelos and Rio Padauiri, according to the data by Van Dam. The position on the map has been indicated accordingly.

60. *Guatteria emarginata* Lobão, Maas & Mello-Silva — Map 14

Guatteria emarginata Lobão, Maas & Mello-Silva (2010) 120, f. 1a–f. — Type: *Vervloet et al. 2316* (holo SPF; iso MBML), Brazil, Espírito Santo, Nova Lombardia, Reserva Biológica Augusto Ruschi, Goipabo Açu, Boeirão, linha de divisa (marco 53 e 52) 600–800 m, 29 Apr. 2003.

Tree c. 17 m tall, diam not recorded; young twigs sparsely covered with appressed, grey hairs, soon glabrous. *Leaves*: petiole 3–4 mm long, c. 1 mm diam; lamina narrowly obovate, 5–9.5 by 1.5–3 cm (leaf index 3.1–3.3), slightly coriaceous, rather



Map 14 Distribution of *Guatteria elegantissima* (●), *G. elongata* (⭘), *G. emarginata* (■), *G. eriopoda* (□), *G. esmeraldae* (◆) and *G. eugeniifolia* (✱).

densely verruculose, shiny, brown above, pale brown below, glabrous above, densely to sparsely covered with appressed hairs below, base attenuate, basal margins revolute, apex emarginate, primary vein impressed above, secondary veins distinct, 9–13 on either side of primary vein, raised above, smallest distance between loops and margin c. 1 mm, tertiary veins inconspicuous, raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 15–30 mm long, 0.5–1 mm diam, densely to sparsely covered with appressed, brown hairs, articulated at 0.2–0.3 from the base, bracts 2–4, soon falling, 5–8 mm long; flower buds broadly ovoid; sepals free, broadly triangular, 4–6 by 6–7 mm, reflexed, outer side densely covered with appressed, brown hairs; petals greenish pink in vivo, broadly elliptic, 5–9 by 6–7 mm, outer side densely covered with appressed, brown hairs; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* and *seed* not seen.

Distribution — Brazil (Espírito Santo).

Habitat & Ecology — In montane, Atlantic forest. At elevations of 600–850 m. Flowering: April; fruiting: unknown.

Vernacular names — Not recorded.

Note — *Guatteria emarginata* is characterized by young twigs covered with grey hairs and narrowly obovate, verruculose leaves with an emarginate apex.

61. *Guatteria eriopoda* DC. — Map 14

Guatteria eriopoda DC. in Dunal (1817) 130; R.E.Fr. (1939) 351, t. 19. — Type: *Dombey s.n.* (holo P; iso F, G, P), Peru, Huánuco, Cuchero ('circa Cochera').

Tree '3-orgyalis'; young twigs densely covered with erect to appressed, curly, white hairs to c. 1 mm long, soon glabrous. *Leaves*: petiole 4–6 mm long, 1–2 mm diam; lamina narrowly elliptic or elliptic-oblong, 12–25 by 4–8 cm (leaf index 3.1–3.5), chartaceous, not verruculose, dull, greyish or brownish black above, brown below, sparsely covered, to densely covered on primary vein, with mostly appressed, curly, white hairs to glabrous at last above, densely to rather densely covered with erect to appressed, curly, white hairs below, base obtuse, apex acuminate (acumen 10–20 mm long), primary vein impressed above, secondary veins distinct, 13–17 on either side of primary vein, impressed above, smallest distance between loops and margin 1–2 mm, tertiary veins flat above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 20–25 mm long, 1–1.5 mm diam, densely covered with erect, more or less curly, whitish to light brown hairs, articulated at 0.2–0.4 from the base, bracts 4–5?, soon falling, only basal ones seen, broadly elliptic(-ovate), 1.5–3 mm long; flower buds broadly ovoid; sepals free, broadly ovate-triangular, 7–8 by 7–8 mm, appressed (as far as seen in young stage), outer side densely covered with appressed to erect hairs; petals colour not recorded, elliptic to obovate, c. 16 by 9 mm, outer side densely covered with appressed to erect hairs; stamens to c. 1.5 mm long, connective shield glabrous. *Monocarps* and *seed* not seen.

Distribution — Amazonian Peru (Huánuco, Loreto).

Habitat & Ecology — Not recorded.

Vernacular names — Not recorded.

Notes — *Guatteria eriopoda* was placed by Fries in sect. *Trichoclonia*.

An incompletely known and perhaps rare species, *G. eriopoda* somewhat resembles the widely distributed *G. ucayalina*, but is distinct from it by the strikingly curly hairs. Note that the long hairs (to c. 1 mm) on the leaves tend to come off earlier than the shorter hairs thus giving the false impression of small-haired leaves (see the Poeppig specimens).

62. *Guatteria esmeraldae* Maas & Westra, *sp. nov.* — Fig. 38; Map 14

Foliis pro genere parvis 15 cm non superantibus atque pedicellis longitudine mediocris monocarpiis brevistipitatis cognita. — Typus: *Neill & QCNE botany interns 12741* (holo U; iso MO, QCNE), Ecuador, Esmeraldas, Muisne, Recinto Palma Junta, 10 km E of Muisne, near road to Tonchique, ridge above Estero La Pedorrera, 1 km N of highway, 100 m, 19 May 2000.

Tree c. 8 m tall, diam not recorded; young twigs sparsely covered with appressed to erect, white hairs to c. 0.2 mm long, soon glabrous. *Leaves*: petiole 2–4 mm long, 1 mm diam; lamina narrowly elliptic, 10–15 by 3–5 cm (leaf index 3–3.3), chartaceous, not verruculose, dull, greyish above, greyish brown below, glabrous above, sparsely covered with appressed hairs below, mainly along primary vein and to c. 0.5 mm long, base acute, apex acuminate (acumen 10–15 mm long), primary vein impressed above, secondary veins distinct, 10–12 on either side of primary vein, impressed above, smallest distance between loops and margin 3–4 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; flowering and fruiting pedicels c. 20 mm long, c. 1 mm diam, sparsely covered with appressed hairs to c. 0.3 mm long, articulated at c. 0.2 from the base, bracts 5–6, soon falling, not seen; flower buds not seen; sepals free, broadly ovate-triangular, c. 3 by 3 mm, appressed, outer side densely covered with appressed hairs; petals pale green in vivo, ovate-triangular, 7–9 by 4–5 mm, outer side densely covered with appressed, white hairs; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* c. 40, bright red in vivo, black in sicco, ellipsoid, 8–9 by 4 mm, sparsely covered with appressed hairs to glabrous, apex rounded, wall c. 0.1 mm thick, stipes 4–6 by 1 mm. *Seed* ellipsoid, c. 8 by 4 mm, brown, transversely grooved, rugose, raphe slightly raised.

Distribution — Ecuador (Esmeraldas).

Habitat & Ecology — In non-inundated, tropical wet forest. At an elevation of c. 100 m. Flowering: May; fruiting: May.

Vernacular names — Not recorded.

Note — *Guatteria esmeraldae*, only known from the type collection, is the smallest-leaved species in the area as far as known. It is best characterized by the combination of relatively small leaves (to c. 15 cm long), fairly long pedicels (to c. 20 mm long), monocarps with stipes less than the monocarp body in length, and the transversely grooved to rugose seeds.

63. *Guatteria eugeniifolia* A.DC. ex R.E.Fr. — Map 14

Guatteria eugeniifolia A.DC. ex R.E.Fr. (1938) 714; (1939) 453. — Type: *Poeppig 1859* (holo G; iso B, BR, F, G, P 2 sheets, W), Peru, San Martín, Tocache Nuevo ('Loreto, Tocache, Maynas'), June 1831.

Tree to c. 20 m tall, to c. 40 cm diam; young twigs densely covered with appressed to more or less erect, curly or not, brown hairs to glabrous, becoming glabrous all over. *Leaves*: petiole 3–10 mm long, 1–2 mm diam; lamina narrowly elliptic, 8–20 by 3–7 cm (leaf index 2.5–3), chartaceous to coriaceous, rather densely to sparsely verruculose, shiny, greyish brown or dark brown above, brown below, glabrous or with some scattered, appressed hairs above, sparsely covered with appressed hairs to c. 1 mm long to glabrous below, base acute to obtuse, the extreme base slightly attenuate, apex acuminate (acumen 5–10 mm long), primary vein flat to impressed above, secondary veins distinct to indistinct, 8–15 on either side of primary vein, raised above, smallest distance between loops and margin 2–4 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or paniculately grouped at the end of a twig by reduction of leaves to bracts; flowering pedicels 12–15 mm long, c. 1 mm diam, fruiting pedicels to c. 25 mm long, 1–2 mm diam, densely covered with erect to more or less appressed, curly, brown hairs to glabrous, articulated at 0.2–0.4 from the base, bracts 5–6, soon falling, not

Fig. 38 *Guatteria esmeraldae* Maas & Westra. Fruiting branch (*Neill et al. 12741*, holotype U).

seen; flower buds not seen; sepals free, broadly ovate-triangular, 4–5 by 4–5 mm, appressed to spreading, outer side densely covered with erect, curly, brown hairs; petals colour not recorded, ovate to elliptic, 12–17 by 5–7 mm, outer side densely covered with erect, curly, brown hairs; stamens c. 1 mm long, connective shield papillate, umbonate. *Monocarps* 10–75, yellowish green when young in vivo, brown in sicco, ellipsoid, 10–13 by 8–11 mm, sparsely covered with appressed hairs to glabrous, apex rounded to apiculate (apiculum < 0.5 mm long), wall 1–1.5 mm thick, stipes 5–7 by 1–1.5 mm. *Seed* ellipsoid, 10–11 by 6–7 mm, shiny brown, smooth to slightly pitted.

Distribution — Amazonian Peru (San Martín).

Habitat & Ecology — In non-inundated forest. At an elevation of 400–500 m. Flowering: June; fruiting: June, November.

Vernacular names — Not recorded.

Note — The taxonomic position of *G. eugeniifolia*, only known from two collections from the Peruvian type locality, needs to be investigated further. The verruculose leaves could possibly point to sect. *Mecocarpus* (Maas & Westra 2011). However, the raised secondary and tertiary venation on the upper side of the leaves and the smooth to slightly pitted (rather than much more sculptured) seeds do not fit at all in this section making a place within that section unlikely. Fries (1939) placed *G. eugeniifolia* in sect. *Tylodiscus*, based on the umbonate staminal shield, setting it apart in that section because of the lack of a sharply delimited glabrous area at the inner base of the inner petals.

64. *Guatteria ferruginea* A.St.-Hil. — Plate 4a; Map 15

Guatteria ferruginea A.St.-Hil. (1825) 38; R.E.Fr. (1939) 398. — Type: *A.F.C.P. de Saint-Hilaire 2* (holo P; iso S), Brazil, Rio de Janeiro, Nova Iguaçu ('prope vicum Aguassu'), July 1816.

Guatteria glazioviana R.E.Fr. (1900) 19, t. 2, f. 1, 2. — Type: *Glaziou 6856* (lecto B selected by Lobão in Maas et al. 2011; isolecto BR, C, G, K, P, S), Brazil, Rio de Janeiro, Novo Friburgo ('Alto da Boa Vista de Nova Friburgo'), 23 Jan. 1874.

Guatteria burchellii R.E.Fr. (1939) 398. — Type: *Burchell 2698* (holo K; iso P), Brazil, Rio de Janeiro, Magé ('Frechal to Magé'), 25 Feb. 1826.

An often cauliflorous tree or shrub 3–10(–18) m tall, 6–18 cm diam; young twigs densely covered with erect, brown hairs. *Leaves*: petiole 6–12 mm long, 2–5 mm diam; lamina narrowly elliptic to narrowly obovate, 17–40 by 5–15 cm (leaf index 1.5–3.8), chartaceous to coriaceous, not verruculose, blackish green above, brown below, sparsely covered with erect hairs to glabrous above, densely covered with erect hairs to sometimes glabrous below, base obtuse to attenuate, apex acuminate (acumen 10–20 mm long), primary vein impressed above, secondary veins distinct, 10–20 on either side of primary vein, raised or impressed above, smallest distance between loops and margin 2–4 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves or mostly in 1–2(–more?)-flowered, densely clustered inflorescences on the stem; pedicels 15–60 mm long, 1–3 mm diam, fruiting pedicels to c. 70 mm long, densely to sparsely covered with erect, brown hairs, articulated at 0.1–0.2 from the base, bracts 2–3, soon falling, 5–6 mm long; flower buds broadly ovoid; sepals free, broadly to shallowly ovate-triangular, 5–10 by 7 mm, reflexed, outer side densely covered with erect hairs to glabrous; petals cream or yellow in vivo, elliptic to ovate, 13–20 by 6–12 mm, outer side sparsely covered with erect, brown hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* 25–55, green, maturing reddish to purple-black in vivo, black in sicco, ellipsoid, 8–12 by 5–7 mm, glabrous, apex apiculate (apiculum 0.5–1 mm long), wall 0.1–0.3 mm thick, stipes 10–25 by 1 mm. *Seed* ellipsoid, 8–12 by 5–7 mm, brown, pitted, raphe raised.

Distribution — Brazil (Bahia, Espírito Santo, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro).

Habitat & Ecology — In periodically inundated or non-inundated forest, on clayey to sandy soil. At elevations of 0–1000 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Not recorded.

Field observations — *A. Rylands 30/1980* (U) from Una, Bahia, Brazil: 'frutos maduros verde amarelados comidos por *Callithrix* e *Leontopithecus*'.

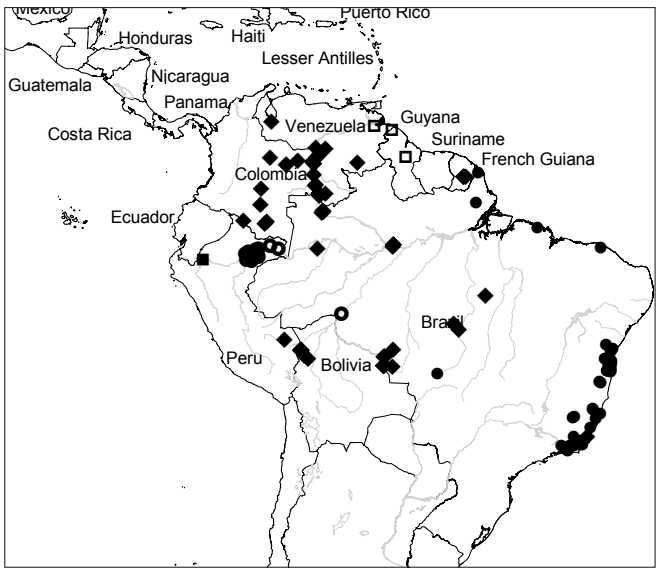
Note — *Guatteria ferruginea* is the only cauliflorous representative of this genus in the Atlantic forests of Brazil. It is characterized by large leaves (17–40 by 5–15 cm), usually densely covered with erect, brown hairs on the lower side, and outer side of sepals and petals also often covered with erect, brown hairs. *Guatteria ferruginea* is similar to *G. pogonopus*. It shares the large leaves, but the pedicels in the latter are much shorter. However, *G. pogonopus* has glabrous leaves and, moreover, it is not cauliflorous.

65. *Guatteria flabellata* Erkens & Maas — Map 15

Guatteria flabellata Erkens & Maas in Erkens et al. (2008) 484, f. 7, pl. 2. — Type: *Maas et al. 6297* (holo U 2 sheets; iso AMAZ, F, K, MO, WIS), Peru, Loreto, Prov. Maynas, Río Momón, 0–5 km above confluence with Río Nanay, 100 m, 15 Nov. 1984.

Guatteria sp. A Vásquez (1997) 100.

Tree (3–)5–28 m tall, to 60 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 8–12(–15) mm long, 3–5 mm diam; lamina narrowly elliptic, 20–38 by 7–16 cm (leaf index 1.6–3.3), coriaceous, not verruculose, dull, brown above and below, glabrous above, sparsely to rather densely covered with appressed, very short hairs below, base cordate to obtuse, apex acuminate (acumen 10–25(–35) mm long), primary vein impressed above, secondary veins distinct, 14–22 on either side of primary vein, impressed above, smallest distance between loops and margin 3–5 mm, tertiary veins slightly raised above, reticulate. *Flowers* in 1–3-flowered inflorescences in axils of leaves or on leafless branchlets; flowering and fruiting pedicels 15–25 mm long, 1–2 mm diam, densely to sparsely covered with appressed, brown hairs, articulated at c. 0.2 from the base, bracts 5–7, soon falling, uppermost bract elliptic, 5–6 mm long, lower bracts broadly elliptic, 1–3 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 5–9 by 4–7 mm, strongly reflexed, outer side densely covered with appressed, brown hairs; petals green, maturing cream or reddish in vivo, obovate to broadly



Map 15 Distribution of *Guatteria ferruginea* (●), *G. flabellata* (⊙), *G. flagelliflora* (■), *G. flexilis* (□) and *G. foliosa* (◆).

Plate 4 a. *Guatteria ferruginea* A.St.-Hil. Stem with flowers and fruit. – b, d, e. *Guatteria goudotiana* Triana & Planch. b. Fruit; d. flowering branch; e. flower. – c, f. *Guatteria heteropetala* Benth. c. Fruiting branch; f. flowering branch. – g. *Guatteria hirsuta* Ruiz & Pav. Fruiting branch. – h, i. *Guatteria inundata* Mart. h. Flowering branch; i. fruiting branch (a: *Amorim et al. 818*; b, d, e: *Sánchez S. et al. 4776*; c: *Stevenson et al. 1115*; f: *Berry s.n.*; g: *Clark et al. 5291*; h: *Croat 19234*; i: *Maas et al. 6288*). — Photos: a, i: P.J.M. Maas; b, d, e: D. Sánchez S.; c: D.W. *Stevenson*; f: P.E. Berry; g: J.L. Clark; h: T.B. Croat.

obovate, 25–40{–50} by 15–25{–40} mm, base distinctly narrowed (unguiculate) and margins rolled outwards, apex often emarginate, outer base densely covered with appressed hairs, middle and apical part sparsely so to glabrous, outer side with distinct, impressed veins; stamens 1–2 mm long, connective shield papillate to hairy. *Monocarps* 50–75, green, maturing red to black in vivo, black in sicco, ellipsoid, 9–15 by 5–8 mm, sparsely covered with appressed hairs, apex apiculate (apiculum < 0.5 mm long), wall 0.2–0.4{–1} mm thick, stipes 8–16 by 0.5–1{–1.5} mm. *Seed* ellipsoid, 8–14 by 5–7 mm, pale to dark brown, pitted to transversely grooved, raphe raised.

Distribution — Amazonian Peru (Loreto), Brazil (Amazonas, Rondônia).

Habitat & Ecology — In periodically inundated forest (igapó, restinga baja, tahuampa, várzea), rarely in non-inundated forest. At elevations of 0–300 m. Flowering: April to December; fruiting: March to November.

Vernacular names — Peru: Anona (*Rimachi Y. 6713*), Anonilla (*Vásquez & Jaramillo 7998*), Anonilla-carahuasca (*Vásquez & Jaramillo 9690*), Baracaspi (*Rimachi Y. 1864*, *6454*), Carahuasca (*Rimachi Y. 3437*, *J. Ruíz & Jaramillo 1134*, *Vásquez & Jaramillo 9434*), Carahuasca blanca (*J. Ruíz 1078*), Carahuasca de bajial, Carahuasca de hoja ancha.

Note — *Guatteria flabellata* is recognizable by petals which are very well marked by a distinct impressed venation on their outer side; furthermore the petals are distinctly narrowed towards the base (almost clawed), whereas the apex is often somewhat emarginate.

66. *Guatteria flagelliflora* Maas & Westra — Map 15

Guatteria flagelliflora Maas & Westra in Erkens et al. (2008) 486, f. 8. — Type: *Vásquez et al. 22500* (holo U 2 sheets; iso F, MO, WAG 2 sheets), Peru, Amazonas, Prov. Condorcanqui, Distr. El Cenepa, Mamayaque, Río Cenepa, Cerro Sakee gaig, 900–1000 m, 12 Feb. 1997.

Tree c. 25 m tall, diam not recorded; young twigs sparsely covered with appressed hairs, soon glabrous, black. *Leaves*: petiole c. 10 mm long, 2 mm diam; lamina narrowly elliptic to narrowly obovate, 23–32 by 9–10 cm (leaf index 2.6–3.6), chartaceous, not verruculose, blackish brown above, brown below, glabrous above, sparsely covered with appressed hairs below, base acute, apex obtuse to acuminate (acumen c. 15 mm long), primary vein flat above, secondary veins distinct, 12–16 on either side of primary vein, slightly raised above, smallest distance between loops and margin 2–4 mm, tertiary veins raised above, reticulate. *Flowers* in condensed panicle-like inflorescences (length not mentioned) on leafless sprouts from the stem; pedicels 15–17 mm long, c. 1.5 mm diam, young fruiting pedicels 15–30 mm long, 2–3 mm diam, densely covered with appressed hairs, articulated at c. 0.2 from the base, bracts 5–6, soon falling, not seen; flower buds depessed ovoid; sepals free, broadly ovate, 5–7 by 4–6 mm, appressed, outer side densely covered with appressed hairs; petals green in vivo, outer ones elliptic to elliptic-ovate, 15–20 by 10–15 mm, inner ones broadly to very broadly elliptic-ovate, 10–15 by 10–12 mm, outer side densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate to hairy. *Monocarps* 25–50, black in vivo, black in sicco, ellipsoid, 8–10 by 4–5 mm, wrinkled in sicco, glabrous, apex apiculate (apiculum < 1 mm long), wall 0.1–0.2 mm thick, stipes 5–8 by c. 1 mm. *Seed* ellipsoid, 9–10 by 4–6 mm, dark brown, rugose, raphe not distinct from rest of seed.

Distribution — Amazonian Peru (Amazonas).

Habitat & Ecology — In primary forest. At elevations of 900–1000 m. Flowering: February; fruiting: February.

Vernacular names — Not recorded.

Note — *Guatteria flagelliflora* is unique by its flagelliform inflorescence, a feature not reported so far in *Guatteria*.

67. *Guatteria flexilis* R.E.Fr. — Fig. 39; Map 15

Guatteria flexilis R.E.Fr. (1952b) 255. — Type: *Forest Department British Guiana 5603* = *Fanshawe 2804* (holo K 2 sheets; iso FDG, K, NY, U), Guyana, Esequibo River, Winiperu Creek, 16 Mar. 1948.

Tree or rarely liana 6–9 m tall, 2.5–12 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 4–6 mm long, c. 1 mm diam; lamina narrowly elliptic, 8–17 by 3–6 cm (leaf index 2.2–3.2), chartaceous, scabridulous, dull, grey to greyish brown above, greyish brown below, youngest leaves densely covered with appressed hairs, soon glabrous above, glabrous below, except for some scattered appressed hairs along primary vein, base attenuate, rarely obtuse, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins distinct, 9–14 on either side of primary vein, impressed to slightly raised above, smallest distance between loops and margin 3–5 mm, tertiary veins flat to slightly raised above, reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; pedicels 25–35 mm long, c. 1 mm diam, fruiting pedicels to c. 50 mm long, c. 2 mm diam, sparsely covered with appressed hairs to glabrous, articulated at 0.1–0.2 from the base, bracts 5–7, soon falling, elliptic, basal ones c. 1 mm long, the upper ones to c. 3 mm long, rarely foliaceous and persisting, to c. 20 mm long; flower buds depressed ovoid; sepals free, broadly to shallowly ovate-triangular, 3–4 by 3–5 mm, appressed, outer side rather densely covered with appressed hairs when young, later becoming almost glabrous, except for the hairy margin; petals pale greyish green or yellow in vivo, oblong to elliptic to narrowly so, 10–26 by 5–10 mm, outer side densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield hairy. *Monocarps* 10–50, green, maturing red, to finally black to purple-black in vivo, black to brown in sicco, ellipsoid, 10–14 by 5–6 mm, glabrous, but apex sparsely covered with appressed hairs, apex rounded to apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 5–10 by c. 1 mm. *Seed* ellipsoid, 9–11 by c. 5 mm, shiny, reddish brown to dark brown, smooth to transversely grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Venezuela (Bolívar, Delta Amacuro), Guyana.

Habitat & Ecology — In non-inundated, primary or secondary forest, the type collection from Greenheart (*Chlorocardium rodiaei*) forest, on sandy or lateritic soil. At elevations of 0–120 m. Flowering: March to May, August, September; fruiting: February, March, May, September.

Vernacular names — Guyana: Black yariyari (Creole name) (*Van Andel et al. 1813*), Karishiri (Arawak name) (*Forest Department British Guiana 6336* = *Fanshawe 3006*). Venezuela: Majagua (*Ang. Fernández 3949*),Yarayara morada (*Marcano-Berti 755*).

Notes — *Guatteria flexilis* is well recognizable by its scabridulous, almost completely glabrous leaves combined with relatively long pedicels of up to c. 50 mm long in fruit.

Fries (1939) placed *G. flexilis* in sect. *Dolichocarpus* and 'most nearly connected with *Guatteria subsessilis*'.

68. *Guatteria foliosa* Benth. — Plate 3f; Map 15

Guatteria foliosa Benth. (1843) 360; Murillo A. & Restrepo (2000) 94; S.A.Mori et al. (2002) 62, pl. 12e; Maas et al. (2007) 639. — Type: *R.H. Schomburgk I 995* (holo K 3 sheets; iso B 3 sheets, BM, E, F 2 sheets, G 3 sheets, K, L, NY, P, U, US), Brazil, Amazonas, Rio Negro, anno 1837.

Tree 4–25 m tall, 5–50 cm diam; young twigs rather densely to sparsely covered with appressed hairs, soon glabrous. *Leaves*:

Fig. 39 *Guatteria flexilis* R.E.Fr. Flowering branch (*Van Andel et al. 1813*, U).

petiole 5–15 mm long, 0.5–1 mm diam; lamina narrowly elliptic to narrowly ovate, or elliptic, 6–16 by 2–6 cm (leaf index 1.9–4) chartaceous, not verruculose, shiny above, dark brown above, pale brown below, glabrous or sometimes sparsely covered with appressed hairs above, but often with appressed to erect, brown hairs along the primary vein above, rather densely to sparsely covered with appressed, brown hairs below, base obtuse, rarely acute, the extreme base long-attenuate, apex acuminate (acumen 5–20 mm long), primary vein flat to impressed above, secondary veins distinct, 6–13 on either side of primary vein, often strongly raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* in 1(–3)-flowered inflorescences in axils of leaves; pedicels 10–30 mm long, 1–2 mm diam, fruiting pedicels to c. 3 mm diam, sparsely covered with appressed hairs, articulated at 0.2–0.3 from the base, bracts 5–6, not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–5 by 3–5 mm, reflexed, outer side densely covered with appressed, pale brown hairs; petals green, maturing yellowish green or brown in vivo, narrowly oblong to narrowly obovate, 10–25 by 4–10 mm, outer side densely covered with appressed, brown hairs; stamens 1–1.5 mm long, connective shield hairy to papillate. *Monocarps* 25–40, green, maturing black in vivo, black to brownish black in sicco, ellipsoid, 5–10 by 3–4 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 10–25 by 0.5–1 mm. *Seed* ellipsoid, 7–8 by 3–4 mm, dark, shiny brown, smooth, raphe not distinct from rest of seed.

Distribution — Amazonian Colombia (Caquetá, Casanare, Vichada), Venezuela (Bolívar, Tachira), French Guiana, Peru (Loreto), Brazil (Amazonas, Mato Grosso, Pará, Rondônia), Bolivia (Beni, Santa Cruz).

Habitat & Ecology — In non-inundated forest, sometimes in campinara forest, or in periodically inundated forest; on sandy to sandy-clayey soil. At elevations of 0–500(–1300) m. Flowering: mainly in September and October; fruiting: February, April, August to October.

Vernacular names — Brazil: Envireira-da-casca-verde (*D. Coêlho INPA 3872*). Colombia: Cïbo dujecu (Muinane name), Carguero negro. Peru: Anonilla (*J. Rodriguez 224*), Carahuasca negra (*J. Ruiz 1073*).Venezuela: Aceituno negro (*J.O. Ramirez & Paredes 46*), Karaurinyek (Pemón language) (*Ang. Fernández 4487*), Majagua (*Breteler 4752*), Majagua verde (*H.L. Clark 7244*, *Liesner 6067*).

Notes — *Guatteria foliosa* is one of the species of this genus most easy to recognize by its long and slender petioles, a mostly obtuse leaf base that is abruptly and long-attenuate at the extreme base, and secondary veins which are strongly raised on the upper side of the lamina.

For differences with *G. liesneri* and *G. maypurensis* see under those species.

Castillo 4328 (MO) from Amazonian Venezuela is aberrant in having pedicels up to c. 45 mm long.

Cid et al. 8344 (U) from Amazonian Brazil deviates in having some of the youngest twigs covered with erect (instead of appressed) to curly hairs.

Farney et al. 1838 (U) from Amazonian Brazil is somewhat aberrant in having sparsely verruculose leaves, a feature not met with in any other specimen of *G. foliosa*.

One collection, *Glaziou 13504* (P: 'Brazil, Minas Gerais, Mar d'Espanha, 8 May 1870') falls quite far out of the distribution of this species. A similar case is that of *Glaziou 13505* (see under *G. inundata*). As Glaziou quite often used erroneous data (see Wurdack 1970), we have the suspicion that the locality data are incorrect.

69. *Guatteria fractiflexa* Maas & Westra — Fig. 36b, 40; Map 16

Guatteria fractiflexa Maas & Westra in Erkens et al. (2008) 491, f. 9. — Type: *Christenhusz & Cárdenas-Ramires 2110* (holo U; iso LZ, TUR, USM), Peru, San Martín, Cerro Guayrapurina, top of the ridge, steep southfacing slope, 1300 m, 14 Aug. 2002.

Liana, shrub, or small tree to c. 4 m tall, diam not recorded; young twigs mostly with a zigzag pattern, sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 3–5 mm long, 1–2 mm diam; lamina narrowly elliptic, 6–15 by 1.5–5 cm (leaf index 3–6), coriaceous, not verruculose, dull, greyish green above, pale brown below, glabrous above, except for some hairs along primary vein, sparsely to rather densely covered with appressed hairs below, base acute to obtuse, slightly oblique, apex long-acute to acuminate (acumen to c. 10 mm long), primary vein impressed above, secondary veins indistinct, 13–20 on either side of primary vein, flat above, smallest distance between loops and margin 1–2 mm, tertiary veins flat above, reticulate. *Flowers* solitary in axils of leaves; pedicels 10–25 mm long, 1–1.5 mm diam, densely covered with erect to appressed, brown hairs, articulated at 0.2–0.6 from the base, bracts 5–6, soon falling, not seen; flower buds broadly ovoid; sepals free to basally connate, broadly ovate-triangular, 5–6 by 5–5.5 mm, appressed, outer side densely covered with erect to appressed, brown hairs; petals pale yellow to yellow in vivo, narrowly elliptic to narrowly elliptic-obovate, 13–15 by 5–6 mm, outer side densely covered with erect to appressed, brown hairs; stamens c. 1.5 mm long, connective shield papillate to glabrous. *Monocarps* black in vivo (according to the label of *Rodriguez et al. 2740*), not seen. *Seed* not seen.

Distribution — Amazonian Ecuador (Zamora-Chinchipe), Peru (Amazonas, Huánuco, San Martín).

Habitat & Ecology — In low, primary forest, with many epiphytes, and with a thick layer of moss, roots and leaves, on sandstone soil. At elevations of 320–2190 m. Flowering: February, May, June, August, November; fruiting: unknown.

Vernacular names — Not recorded.

Notes — *Guatteria fractiflexa* is with *G. scandens* (and sometimes *G. beckii*, *G. flexilis* and *G. synsepala*) one of the five liana species in the genus. A noteworthy feature is the zigzag pattern of the lateral (plagiotropic) branchlets, most extreme in Amazonian Peru (Amazonas and San Martín), but less pronounced in collections from Peru, Huánuco (*Schunke V. 10299*) and Ecuador, Zamora-Chinchipe (*Jørgensen et al. 2304*).

Pirie et al. 130 (Peru, Amazonas; sterile liana) should be mentioned here: it resembles collections of *G. fractiflexa*, but it differs by branchlets, petioles and lower leaf sides all densely covered with erect hairs to c. 1 mm long. We have decided to leave it out as the number of collections of *G. fractiflexa* is too low to have a good picture of the variability of this curious species.

70. *Guatteria friesiana* (W.A.Rodrigues) Erkens & Maas — Map 16

Guatteria friesiana (W.A.Rodrigues) Erkens & Maas (2008) 404; Maas & Westra (2011) 123, f. 8a, 9, pl. 1c. — *Guatteriopsis friesiana* W.A.Rodrigues (1981) 49, f. 1; Maas et al. (2007) 644. — Type: *D.F. Coêlho INPA 3609* (holo INPA; iso S), 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 to c. 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, scabridulous, pale green to greyish green on both sides, glabrous above, sparsely

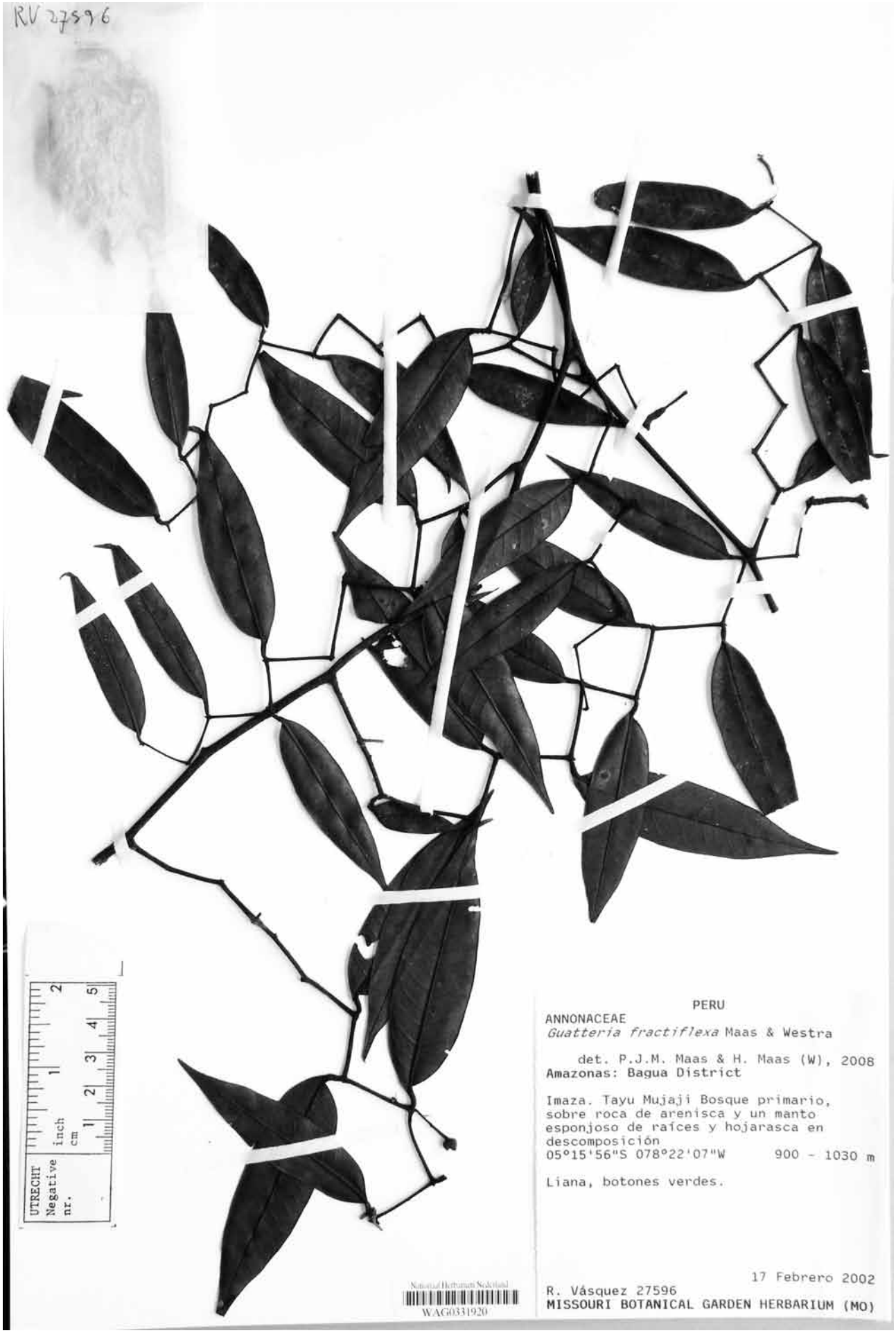


Fig. 40 *Guatteria fractiflexa* Maas & Westra. Flowering branch (*Vásquez 27596*, WAG).

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, smallest distance between loops and margin 2–5 mm, tertiary veins inconspicuous and hardly visible, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; flowering and fruiting 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 by 6–7 mm, appressed, soon becoming spreading to reflexed, outer side densely covered with dark brown, appressed hairs; petals cream in vivo, unequal, narrowly ovate-triangular to narrowly oblong-ovate, outer ones 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, brown in sicco , ellipsoid, 19–23 by 6–7 mm, sparsely covered with appressed and erect hairs, apex apiculate (apiculum c. 2 mm long), wall 0.1–0.2 mm thick, stipes 1–3 by 2 mm. *Seed* ellipsoid, 13–19 by 6–8 mm, dark, shiny brown, slightly transversally grooved, slightly pointed at the apex, raphe strongly impressed.

Distribution — Amazonian 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 name — Brazil: Envireira (*Rodrigues & Loureiro 5908*).

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

71. *Guatteria galeottiana* Baill. — Map 16

Guatteria galeottiana Baill. (1868b) 268; R.E.Fr. (1939) 373, f. 10b–d. — Type: *Liebmann 16* (holo C; iso P), Mexico, Oaxaca, Comaltepec, Aug. 1842.

Tree 2–10 m tall, 10–20 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 4–8 mm long, 1–2 mm diam; lamina narrowly elliptic, rarely obovate, 10–15 by 3–5 cm (leaf index 3–3.3), chartaceous, not verruculose, shiny, often bright green when dry above and below, glabrous above, glabrous below, except for some hairs along the primary vein, base attenuate, apex acuminate (acumen 10–20 mm long), primary vein flat above, secondary veins distinct, 8–15 on either side of primary vein at almost right angles, slightly raised above, smallest distance between loops and margin 2–4 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 10–30 mm long, c. 1 mm diam, fruiting pedicels 35–50 mm long, c. 2 mm diam, sparsely covered with appressed hairs to glabrous, articulated at c. 0.2 from the base, bracts 5–7, soon falling; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–5 by 4–5 mm, reflexed, outer side rather densely covered with appressed hairs; petals yellowish green to yellow in vivo, ovate, 12–15 by 6–7 mm, outer side rather densely covered with appressed hairs; stamens 1–2 mm long, connective shield papillate. *Monocarps* 10–20, green, maturing blackish purple in vivo, black in sicco, narrowly ellipsoid, 10–13 by 5–6 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall c. 0.2 mm thick, stipes 9–17 by 1 mm. *Seed* ellipsoid, 9–12 by 4–5 mm, dark brown, rugose, raphe not distinct from rest of seed.

Distribution — Mexico (Oaxaca, Veracruz).

Habitat & Ecology — In forest ('selva alta perennifolia'). At elevations of 0–1400 m. Flowering: June, October, November; fruiting: February, April, November.

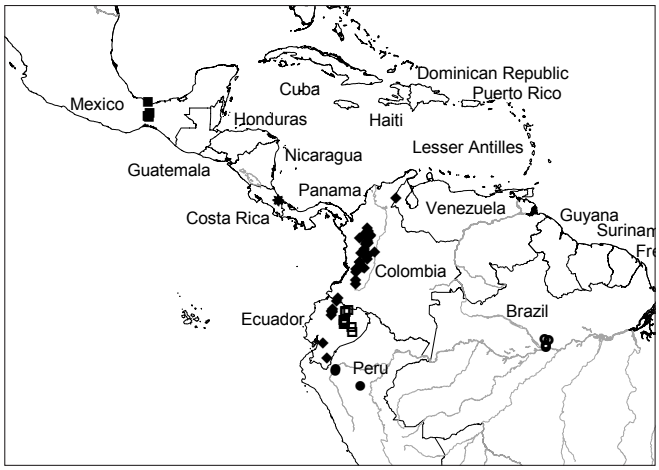
Vernacular names — Mexico: Peseu (Zoque language), Zapote de monte (*Osorio et al. 17*, *Rincón G. et al. 700*).

Note — *Guatteria galeottiana* is an endemic from the Veracruz and Oaxaca regions in Mexico. It can be recognized by its leaves that often dry bright green, its long pedicels, the narrowly ellipsoid and apiculate monocarps, and its almost perpendicular secondary venation. All these characters fit the type very well. However, the collections from Oaxaca (e.g., *H. Hernández G. 1695*) differ somewhat by having rounder monocarps and a somewhat more ascending secondary venation, but otherwise fall within the description of this species.

72. *Guatteria gentryi* Maas & Erkens — Map 16

Guatteria gentryi Maas & Erkens in Erkens et al. (2008) 495, f. 10, pl. 3. — Type: *Gentry 12444* (holo MO 2 sheets; iso U), Ecuador, Sucumbíos, 17 km W of Lumbaque (70 km W of Lago Agrio), 1130 m, 4 Nov. 1974.
Guatteria sp. 8 Chatrou et al. (1997) 110.

Tree 5–40 m tall, 10–40 cm diam; young twigs sparsely covered with appressed hairs, very soon glabrous. *Leaves*: petiole 6–12 mm long, 2–3 mm diam; lamina narrowly elliptic, 14–25 by 4–8 cm (leaf index 2.8–4), chartaceous, not verruculose, dull, greenish brown above, not or sometimes slightly verruculose below, brownish below, glabrous above, rather densely covered with appressed hairs in the youngest stages but very soon becoming almost completely glabrous below, base acute to obtuse, apex acuminate (acumen 5–15 mm long, its apex itself obtuse), primary vein slightly raised above, secondary veins distinct, 10–13 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins flat to slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 4–8 mm long, 1.5–2 mm diam, fruiting pedicels 5–10 mm long, 3–4 mm diam, densely covered with appressed hairs, articulated at 0.5–0.6 from the base, bracts 5–7, soon falling, the two uppermost ones broadly ovate, to c. 8 mm long; flower buds broadly ovoid; sepals free or basally connate, broadly ovate, 5–6 by c. 5 mm, appressed to spreading, outer side densely covered with appressed hairs; petals green, maturing dull yellow, yellow or cream in vivo, ovate, elliptic to oblong-ovate, 12–20 by 6–9 mm, outer side densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate to hairy. *Monocarps* 10–30, green, maturing black in vivo, black, rarely brown in sicco, ellipsoid, 15–20 by



Map 16 Distribution of *Guatteria fractiflexa* (●), *G. friesiana* (⊙), *G. galeottiana* (■), *G. gentryi* (□), *G. goudotiana* (◆) and *G. herrerana* (✳).

8–14 mm, rather densely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 1 mm long), wall 0.5–1.5 mm thick, stipes 7–18 by 1–2 mm. *Seed* ellipsoid, 15–19 by 8–10 mm, brown, longitudinally and transversely grooved to rugose, raphe not distinct from rest of seed.

Distribution — Amazonian Ecuador (Napo, Pastaza, Sucumbíos), Peru (Amazonas).

Habitat & Ecology — In non-inundated, primary, sometimes premontane, wet forest, on clayey, red soil. At elevations of 300–1300 m. Flowering: March to May, September to November; fruiting: throughout the year.

Vernacular name — Ecuador: Cara huasca (Quichua) (*Freire & Cerda 165*).

Note — *Guatteria gentryi* can be recognized by a primary vein which is slightly raised on the upper side of the lamina, a feature very rarely met with in species of *Guatteria*. Further noteworthy aspects are the strongly grooved seeds, which makes them resemble miniature brains. The flowers and fruits are very shortly pedicellate.

73. *Guatteria goudotiana* Triana & Planch. — Plate 4b, d, e; Map 16

Guatteria goudotiana Triana & Planch. (1862) 33; R.E.Fr. (1939) 394. — Type: *Triana s.n.* (lecto P, selected by Fries 1939), Colombia, Quindio ('Prov. Marequita, forêts du Quindio').

Guatteria quinduensis Triana & Planch. (1862) 34; R.E.Fr. (1939) 393, syn. nov. — Type: *Triana s.n.* (holo P; iso BM), Colombia, Antioquia ('prov. de Antioquia'), without location, 2000 m.

Guatteria heterotricha R.E.Fr. (1939) 392, t. 25, syn. nov. — Type: *Purdie s.n.* (holo K; iso K), Colombia, Huila, Neiva ('woods near Neiva'), July 1846.

Guatteria lehmannii R.E.Fr. (1939) 395, syn. nov. — Type: *Lehmann 4616* (holo B; iso BM, F, GH, K, US), Colombia, Antioquia, Aguadas, 2000–2300 m.

Guatteria coriacea R.E.Fr. (1939) 527, f. 38c, syn. nov. — Type: *Purdie s n.* (holo K), Colombia, without location.

Tree or rarely a shrub 3–25 m tall, 8–40 cm diam; young twigs often zigzagging, rather densely to sparsely covered with appressed, curly, brown hairs, finally becoming glabrous. *Leaves*: petiole 4–8 mm long, 1.5–2 mm diam; lamina narrowly elliptic to elliptic, rarely narrowly obovate, 7–19 by 2.5–8 cm (leaf index 2–2.9), coriaceous, rarely chartaceous, not or rarely sparsely verruculose, dull to shiny, greyish green, greyish, or brown above, greenish, greyish green, or brown below, glabrous above, except for a few scattered appressed, brown hairs, sparsely covered with appressed, brown hairs to glabrous below, base acute to attenuate, basal margins often revolute, apex acuminate (acumen 5–15 mm long), rarely acute, primary vein impressed to flat above, secondary veins distinct, 10–16 on either side of primary vein, slightly raised above, smallest distance between loops and margin 2–5 mm, tertiary veins slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescence in axils of leaves; pedicels 10–30 mm long, 1–2 mm diam, fruiting pedicels 2–2.5 mm diam, rather densely to sparsely covered with appressed, brown hairs, articulated at 0.2–0.4 from the base, bracts 5–7, soon falling, the basal ones c. 8 mm long, the 2 upper ones 10–14 mm long; flower buds broadly to depressed ovoid; sepals free, broadly ovate-triangular, 3–7 by 3–8 mm, spreading, outer side rather densely to sparsely covered with appressed, brown hairs; petals greyish to black in vivo, elliptic or ovate, 10–20 by 5–11 mm, outer side densely covered with appressed, brown hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 15–35, green, maturing purple-black to black in vivo, dark brown or black in sicco, ellipsoid, 10–20 by 6–9 mm, sparsely covered with appressed, brown hairs, soon glabrous, apex rounded to apiculate (apiculum 0.2–1 mm long), wall 0.2–0.5 mm thick, stipes 7–18 by 1–3 mm. *Seed* ellipsoid, 10–17 by 6–8 mm, shiny, reddish brown, rugulose to pitted, raphe raised.

Distribution — Colombia (Antioquia, Huila, Nariño, Quindio, Tolima, Valle del Cauca), Ecuador (Imbabura, Napo, Pichincha, Zamora-Chinchipe).

Habitat & Ecology — In montane or premontane forest, with *Quercus humboldtii* ('Roble'), on slopes, along roadsides and in pasture vegetation (disturbed forest). At elevations of 960–2450(–3000) m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Colombia: Cargadero (*López-Figueiras 8409*), Garrapata (*Purdie s.n.*), Garapatta (*Purdie s.n*).

Uses — Colombia: Bark used for tying ('Corteza utilizadas para amarrar') (*Silverstone-Sopkin 901*).

Notes — *Guatteria goudotiana* is one of the few species of *Guatteria* which occurs at high elevations (premontane and montane forests) in Colombia and Ecuador. It is easily recognized by coriaceous leaves with revolute margins (very well observed in the field), spreading sepals and greyish to black petals, a feature rarely seen in *Guatteria*.

Alzate 1075 (U) from Turbo, Antioquia, Colombia is the only specimen examined that occurs in lowlands, at 30 m elevation.

Cuatrecasas 22297 (F, S, US) from 'Monte el Tabor', Valle del Cauca, Colombia is aberrant by having relatively larger monocarps (c. 20 by 15 mm) with a thicker wall of c. 2 mm.

D.A. Sánchez S. 566, *1255*, *1285*, *1351* (MEDEL, U) from the upper Basin of Cuevas River in the Murri region (Antioquia, Colombia) were wrongly indentified (Sánchez S. 1993) as *G. chocoensis* (now a synonym of *G. hirsuta*) which differs from *G. goudotiana* by having an indument of erect hairs and relatively small monocarps

74. *Guatteria grandiflora* Donn.Sm. — Fig. 41; Map 17

Guatteria grandiflora Donn.Sm. (1889) 25; R.E.Fr. (1939) 523, t. 36. — Type: *Donnell Smith 1235* (syn B, GH, K, P, US 2 sheets), Guatemala, Alta Verapaz, Pansamalá, 1100–1200 m, May 1887.

Guatteria anomala R.E.Fr. (1939) 524, f. 1a–f. — Type: *Von Tuerckheim 7816* (holo B; iso GH, K, M, NY, US 2 sheets), Guatemala, Alta Verapaz, Cubilguïtz ('Cubilquitz'), 350 m, May 1901.

Tree 6–60 m tall, up to 170 cm diam and with deeply fluted stems; young twigs rather densely covered with appressed, white hairs, soon glabrous. *Leaves*: petiole 2–9 mm long, 1–4 mm diam; lamina narrowly elliptic to narrowly obovate, 10–27 by 3–8 cm (leaf index 2.6–3.8), chartaceous, rather densely verruculose to not verruculose, dull, grey to brown above, brown below, glabrous above, glabrous below, the primary vein rather densely covered with erect to appressed white long hairs to glabrous below, base obtuse to attenuate, apex acuminate (acumen 2–10 mm long), primary vein impressed to flat above, secondary veins distinct, 9–17 on either side of primary vein, slightly raised to raised above. *Flowers* terminal, solitary or in up to several-flowered, paniculate-like inflorescences, also axillary; pedicels 10–65 mm long, 1–2 mm diam, sparsely covered with appressed, white hairs, articulated at 0.1–0.2 from the base, thickened above the articulation, bracts 2–3 (?) to a pedicel in terminal flowers, or c. 7 on pedicels of axillary flowers, soon falling, not seen; flower buds depressed ovoid, slightly pointed; sepals free, broadly ovate-triangular, 4–10 by 4–7 mm, reflexed, outer side densely covered with appressed and erect, curly, white hairs; petals green with red inner base in vivo, narrowly oblong-ovate to narrowly ovate, 12–40 by 5–13 mm, outer side densely covered with appressed and erect, curly, white hairs; stamens (1–)1.5–3 mm long, connective shield papillate. *Monocarps* 5–40, red, maturing black in vivo, black in sicco, narrowly ellipsoid to ellipsoid, 15–30 by 8–12 mm, glabrous, apex rounded to slightly apiculate, stipes 4–15 by 2–3 mm. *Seed* ellipsoid, 15–25 by 8–12 mm, pale brown to dark brown, rugulose.

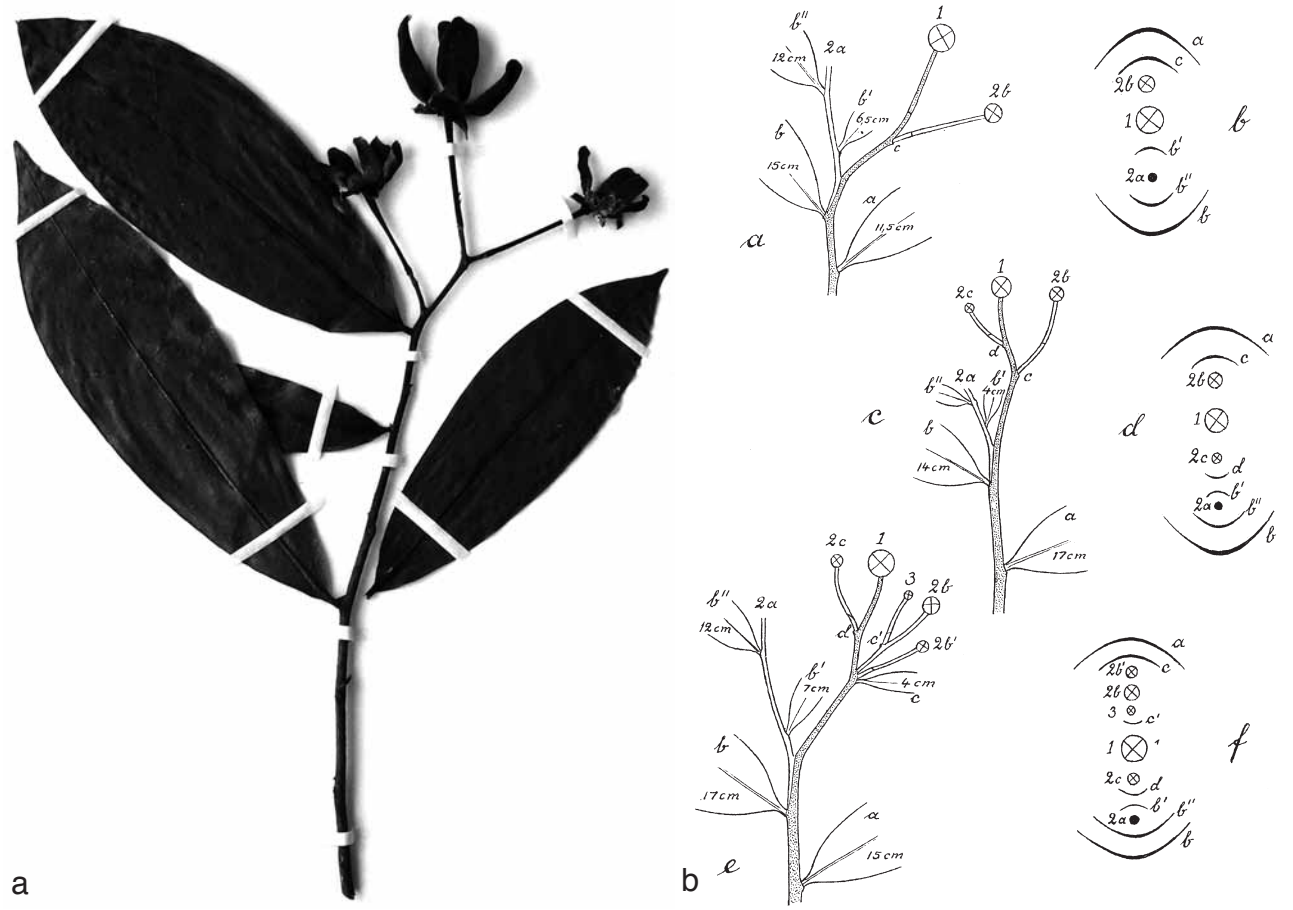


Fig. 41 *Guatteria grandiflora* Donn.Sm. a. Flowering branch; b. analysis of concaulescence in three inflorescences bearing 2, 3 and 5 flowers, respectively, with corresponding diagrammatic cross sections; main axis stippled (a: *Méndez G. 6051*, U; b: after Fries 1939: f. 1 (as *G. anomala* R.E.Fr.)).

Distribution — Mexico (Chiapas, Oaxaca, Veracruz), Guatemala, Honduras.

Habitat & Ecology — In forest. At elevations of 0–3150 m. Flowering: April, May, July; fruiting: May, July, August.

Vernacular names — Guatemala: Pale-max (*Kunkel 18*, *355*, *411*, *420*, *440*). Mexico: Candelero (*Caletti 170*), Candilero (*Wendt et al. 3330*), Corcho negro, Ijkbat, Jooncu'y (Zoque name) (*Caletti 170*), Palo de chombo (*Miranda 7176*), Palo de zope, Palo de zopo, Zopo.

Note — *Guatteria grandiflora* apart from being among the few species in the genus with terminal flowers is remarkable by the partial fusion of axes leading to the panicle-like arrangement of flowers at the end of branchlets in part of the representatives. There exists a good illustration of this (Sargent 1905). This phenomenon is not known to occur in any other *Guatteria* species, and it led Fries (1939) to create a separate species, *G. anomala*. See also the introduction and Fries's excellent analysis (Fig. 14b). When examining material of both species we had the impression that not only the arrangement of the flowers but also other characters, e.g., presence or absence of verruculae, the long appressed hairs on the primary vein below, could distinguish the two. Closer inspection showed quite a bit of overlapping though, leaving only the fusion of axes in the inflorescence to go by. Given an otherwise homogenous impression of all specimens taken together, we think that there is insufficient support for a two-species concept.

75. *Guatteria grandipes* Maas & Westra — Map 17

Guatteria grandipes Maas & Westra in Erkens et al. (2008) 497, f. 11; Maas & Westra (2011) 127. — Type: *Stein et al. 4002* (holo MO; iso F, 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, forming a marginal vein, at a smallest distance of 2–3 mm from the margin, tertiary veins inconspicuous, flat above, slightly percurrent. *Flowers* solitary in axils of leaves; flowering and fruiting pedicels 40–90 mm long, c. 1 mm diam, densely to rather densely covered with erect, rough, brown hairs ('hirsute') 1.5–2.5 mm long, articulated at c. 0.1 from the base, bracts soon falling, not seen; flower buds subglobose; sepals free, ovate, 11–12 by c. 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 papillate. *Monocarps* c. 15, green in vivo, brown in sicco, ellipsoid, 15–16 by c. 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 c. 1 mm. *Seed* ellipsoid, 15–16 by 7 mm, pale brown, rugose, raphe not distinct from rest of seed.

Distribution — Amazonian Peru (Loreto).

Habitat & Ecology — In forest (the type collection from 'swampy forest'), on lateritic to clayey soil. At elevations of 120–150 m. Flowering: August; fruiting: January, August.

Vernacular names — Not recorded.

Note — *Guatteria grandipes* falls within Fries's sect. *Mecocarpus* by its verruculose leaves, provided with a marginal vein. It differs from all species of that section by extremely long pedicels of up to c. 90 mm long.

76. *Guatteria griseifolia* Maas & Westra — Map 17

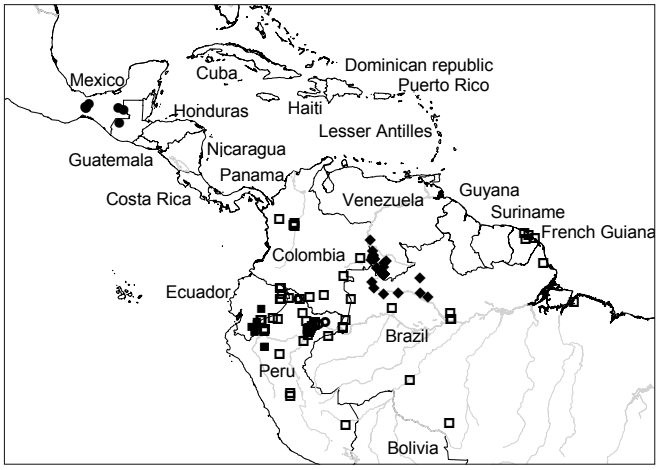
Guatteria griseifolia Maas & Westra (2011) 127, f. 8b, c, 10. — Type: *Gentry et al. 30941* (holo U 2 sheets; iso MO), Ecuador, Morona-Santiago, Campamento La Playa, road construction camp 23 km SE of San Juan Bosco, 1050 m, 28 Jan. 1981.
Guatteria sp. 4 Chatrou et al. (1997) 110.

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 acuminate (acumen to c. 15 mm long), primary vein impressed to slightly raised at the base 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 slightly raised above, reticulate. *Flowers* in 1–2(–several)-flowered inflorescences in axils of leaves or on leafless 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 uppermost bract broadly elliptic, 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 or brownish yellow in vivo, ovate to broadly 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 or green, maturing dark purple to black in vivo, black in sicco, ellipsoid, 10–17 by 5–6 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 1–3 by c. 1 mm. *Seed* ellipsoid, 10–15 by 4–7 mm, shiny brown, rugose, raphe raised.

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

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

Vernacular names — Not recorded.



Map 17 Distribution of *Guatteria grandiflora* (●), *G. grandipes* (⭘), *G. griseifolia* (■), *G. guianensis* (□) and *G. heteropetala* (◆).

Note — *Guatteria griseifolia* occurs at quite high elevations in Ecuador and Peru. It can be distinguished by the often winged young twigs, greyish green leaves, a leaf apex varying from obtuse, rounded to acuminate, and an often keeled midrib.

77. *Guatteria guianensis* (Aubl.) R.E.Fr. — Map 17

Guatteria guianensis (Aubl.) R.E.Fr. (1939) 505, f. 32a–c; Maas et al. (2007) 639; Maas & Westra (2011) 127, f. 11, 12, pl. 1d–f. — *Aberemoa guianensis* Aubl. (1775) 610, t. 245. — *Guatteria aberemoa* Dunal (1817) 126, nom. illeg. — Type: *Aublet s.n.* (lecto BM, selected by Fries 1939), French Guiana, 'in silvis remotis Sinemariensibus'.
Guatteria aberemoa Dunal var. *microcarpa* DC. (1817) 502. — Type: not seen.
Guatteria multivenia Diels (1927) 171. — Type: *Tessmann 5192* (holo B; iso F, G, NY), Peru, Loreto, Lower Río Itaya, Soledad, 110 m, 13 June 1925.
Guatteria excellens R.E.Fr. (1938) 721. — Type: *Klug 1273* (holo F; iso NY, US), Peru, Loreto, Mishuyacu, near Iquitos, 100 m, Apr. 1930.
Guatteria calophylla R.E.Fr. (1939) 507, f. 32d–f. — Type: *Krukoff 1534* (holo S; iso BM, F, G, K, NY, P, U, US), Brazil, Mato Grosso, source of Rio Jatuarana, Machado River region, 5 Dec. 1931.
Guatteria robusta R.E.Fr. (1957a) 328. — Type: *Fróes 20788* (holo NY; iso IAN), 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 to c. 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, extreme base a rounded lobule on each side, apex acuminate (acumen 5–30 mm long and ending in an acute tip), primary vein impressed above, secondary veins 20–35 on either side of primary vein, impressed above, forming a marginal vein, at a smallest distance of 1–7 mm from the margin, tertiary veins flat to raised above, percurrent. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 12–25 mm long, 2–3 mm diam, fruiting pedicels to c. 35 mm long, c. 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 uppermost bract elliptic, 7–8 mm long; flower buds broadly ovoid, acute; sepals almost free, broadly ovate-triangular, 7–12 by 8–11 mm, spreading 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, rugulose, longitudinally and transversely grooved, raphe not distinct from rest of seed.

Distribution — Colombia (Amazonas, Antioquia, Vaupés), French Guiana, Ecuador (Napo, Sucumbios), Peru (Amazonas, Loreto, Madre de Dios, Pasco, San Martín), 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*). Colombia: Muecantokaro-

riká (Makuna name) (*García-Barriga 14374*), Pö-ö-ká-no (Gwanano name) (*Schultes & Cabrera R. 19320*), Pweé-ka-no (Tukano and Desano name) (*Schultes & Cabrera R. 19320*). Ecuador: Moncapatamo (Huaorani name) (*M. Aulestia & Bainca 3533*, *M. Aulestia & Omehuat 3209*), Yaris (Shuar name) (*Morales et al. 1466*). French Guiana: Abéremou (Galibi), Mamanyaré (Creole name), Pomme canelle (Creole name). Peru: Carahuasca (*P. Díaz et al. 85*, *Vásquez et al. 5968*), Churum yeis (*Huashikat 832*, *1046*), Espintana (*Rimachi Y. 7515*), Wáshi yéis (*Huashikat 665*), Wasri yais (Shuar name) (*Tunqui 857*), Wuáshi yais (Shuar name) (*Leveau 250*).

Uses — Peru: Wood used for construction of houses ('Se utiliza la madera para la casa') (*Huashikat 1046*).

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 to c. 0.5 mm long in *G. guianensis* vs erect to half-appressed, stiff hairs to c. 3 mm long in *G. decurrens*.

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

78. *Guatteria herrerana* N.Zamora & Maas, *sp. nov.* — Fig. 36c, 42; Map 16

Inter speciebus Centroamericanis unica habitu cauliflоro vel ramiflоro. — Typus: *G. Herrera C. 8401* (holo CR; iso L), Costa Rica, Limón, Limón, Almirante, Cerro entre la cuenca superior del Río Xikiari ('Xichiary') y la del Río Boyei, 1200 m, 11 Aug. 1995.

Tree c. 7 m tall, c. 12 cm diam; young twigs densely covered with erect hairs, soon glabrous. *Leaves*: petiole 8–10 mm long, 2–3 mm diam; lamina elliptic to oblong-elliptic, 6–16 by 3–6 cm (leaf index 2–2.6), chartaceous, not verruculose, dull, brown above, brown below, sparsely covered with erect hairs above, sparsely to rather densely covered with erect, brown hairs below, base obtuse, apex acuminate (acumen 10–20 mm long), primary vein impressed above, secondary veins distinct, 8–12 on either side of primary vein, impressed above, smallest distance between loops and margin 1–2 mm, tertiary veins slightly raised above, reticulate to slightly percurrent. *Flowers* in 1–2-flowered inflorescences, on leafless branchlets or on the stem; pedicels 10–25 mm long, c. 1 mm diam, fruiting pedicels c. 2 mm diam, densely covered with erect, brown hairs, articulated at c. 0.1 from the base, bracts soon falling, not seen; flower buds not seen; sepals free, broadly ovate-triangular, 6–7 by 7–8 mm, appressed, outer side densely covered with appressed hairs; petals yellow in vivo, oblong-elliptic, 10–15 by 6–10 mm, outer side densely covered with appressed, brown hairs; stamens not seen. *Monocarps* c. 25, green in vivo, black in sicco, ellipsoid to ovoid, 11–12 by 8–9 mm, glabrous, apex bluntly apiculate (apiculum 1–2 mm long), wall 0.1–0.2 mm thick, stipes 21–23 by 1–2 mm. *Seed* ovoid to ellipsoid, c. 10 by 7 mm, brownish red, pitted.

Distribution — Costa Rica (Limón).

Habitat & Ecology — In non-inundated forest on hilly terrain. At an elevation of c. 1200 m. Flowering: August; fruiting: August.

Vernacular names — Not recorded.

Field observations — Flowers with nice smell ('flor de aroma muy agradable') (*G. Herrera C. 8401*).

Note — *Guatteria herrerana*, only known from the type collection, is unique among the Central American species in being cauliflorous to ramiflorous. Its relationship needs additional study.

79. *Guatteria heteropetala* Benth. — Plate 4c, f; Map 17

Guatteria heteropetala Benth. (1843) 360; R.E.Fr. (1939) 538; Erkens & Maas (2008) 405. — *Heteropetalum brasiliense* Benth. (1860) 69; R.E.Fr. (1930) 74, t. 2. — Type: *R.H. Schomburgk 1 950* (holo K; iso B, BM 2 sheets, F, G 2 sheets, K, L, P, U), Brazil, Amazonas, Rio Negro, anno 1839.

Heteropetalum spruceanum R.E.Fr. (1930) 75, t. 3. — Type: *Spruce 3184* (holo B; iso BM, BP, C, E, G 3 sheets, K, MG, NY, P), Venezuela, Bolívar, Río Pasíba ('Vasiva'), affluent of Río Casiquiare, Dec. 1853.

Heteropetalum spruceanum R.E.Fr. var. *longipetalum* R.E.Fr. (1957a) 330. — Type: *Maguire et al. 36261* (holo NY; iso S), Colombia, Guainía, Río Atabapo, between San Fernando de Atabapo and Cacagual, 18 Nov. 1953.

Tree 3–6 m tall, to c. 4 cm diam, sometimes several-stemmed (*O. Huber & Medina 5818*), young twigs sparsely covered with appressed hairs, very soon glabrous. *Leaves*: petiole 8–22 mm long, 1–3 mm diam; lamina narrowly elliptic to narrowly oblong-elliptic, 6–18 by 2–6.5 cm (leaf index 2–4.7), coriaceous, not verruculose, dull, greyish or brownish green above, brown or brownish green below, glabrous above, sparsely covered with appressed hairs to glabrous below, base attenuate, apex acute, acuminate (acumen 5–15 mm long) or obtuse, primary vein impressed, flat, or more or less raised above, secondary veins distinct, 11–15 on either side of primary vein, slightly raised above, smallest distance between loops and margin 1–2.5 mm, tertiary veins raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves, sometimes accompanied by lateral shoot from axial bud; pedicels 5–10 mm long, 1.5–2 mm diam, fruiting pedicels to c. 15 mm long, c. 2.5 mm diam, rather densely to sparsely covered with appressed hairs, articulated at 0.2–0.4 from the base, bracts 5–6, soon falling, the 2 uppermost still present at flowering time, broadly elliptic, c. 2 mm long at the base to 6 mm long at the top; flower buds conical; sepals free, broadly ovate to broadly ovate-triangular, acuminate, 6–7 by 5–6 mm, appressed, outer side densely covered with appressed hairs; petals yellow or reddish yellow in vivo, strongly unequal, narrowly ovate to ovate, outer ones 7–12 by c. 4 mm, outer side densely covered with appressed hairs, inner ones 13–32 by 8–13 mm, outer side densely to rather densely covered with appressed hairs; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* 2–13, reddish to reddish violet in vivo, black to brown in sicco, ellipsoid to narrowly ellipsoid, 12–22 by 6–12 mm, smooth or somewhat longitudinally ridged, sparsely covered with appressed hairs, soon glabrous, apex rounded to slightly hard-pointed, wall 0.2–0.5 mm thick, stipes 0–2 by 0–2 mm. *Seed* ellipsoid, 13–18 by 6–7 mm, pale brown, pitted to transversely grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Colombia (Guainía),Venezuela (Amazonas), Brazil (Amazonas).

Habitat & Ecology — In periodically inundated, black water-flooded igapó forest. At elevations of up to 125 m. Flowering: March, July to December; fruiting: January, February, May.

Vernacular names — Venezuela: Majagua (*Maguire et al. 36261*, *Velazco 1883*), Palo de boya negro (*O. Huber & Medina 5818*).

Note — *Guatteria heteropetala* is one of the few species in the genus occurring in periodically inundated forests. It is easily recognizable by strongly unequal petals, the inner ones being almost twice as long as the outer ones. This was the main reason why this taxon was placed by earlier authors in the segregate genus *Heteropetalum*. Recent research (Erkens et al. 2009) proved, however, that it should better be merged into *Guatteria*.

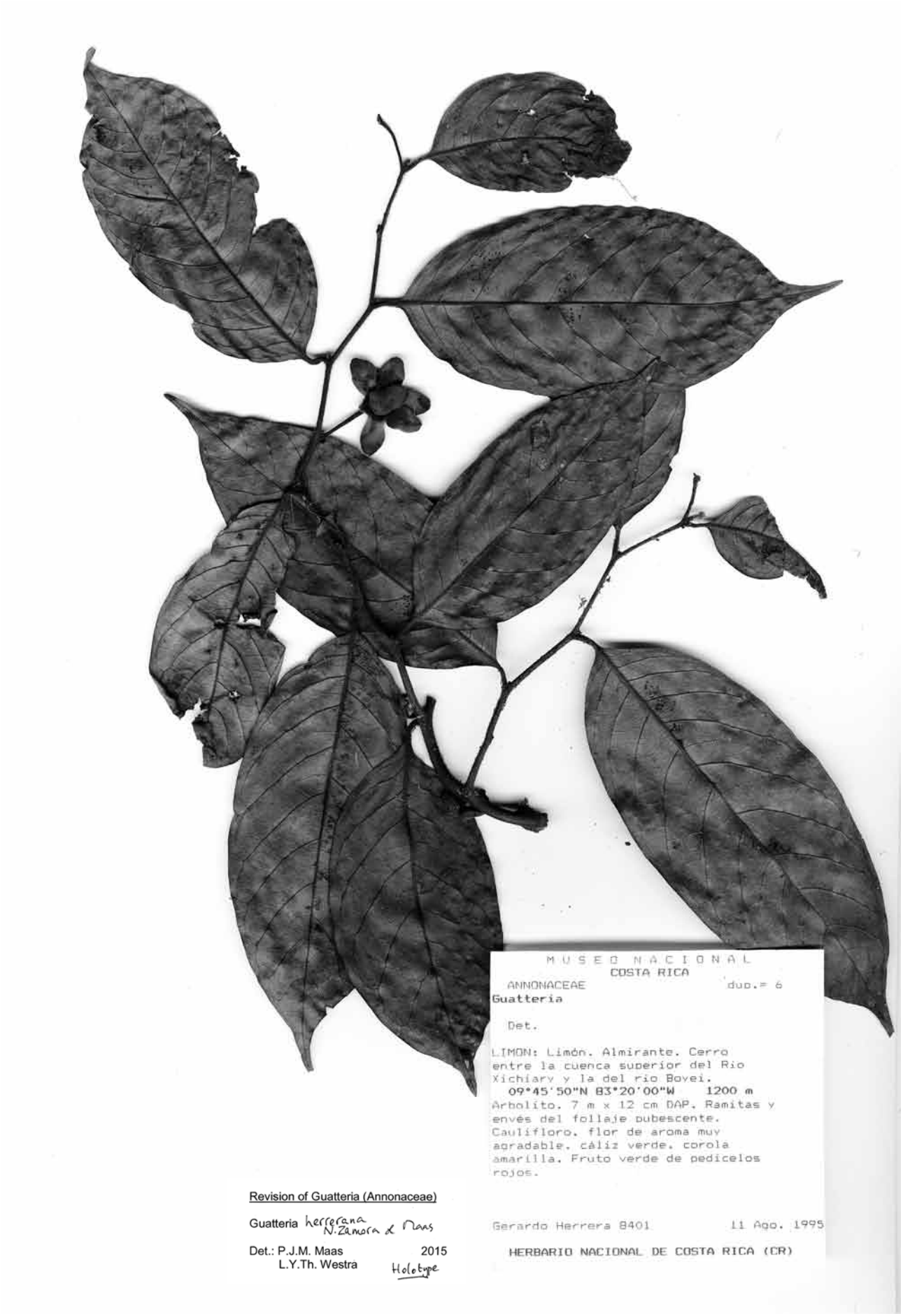


Fig. 42 *Guatteria herrerana* N.Zamora & Maas. Flowering branch (*G. Herrera C. 8401*, holotype part CR).

80. *Guatteria hirsuta* Ruiz & Pav. — Fig. 36d, e, 43; Plate 4g; Map 18

Guatteria hirsuta Ruiz & Pav. (1798) 146; R.E.Fr. (1939) 369, f. 9b. — Type: *Ruiz s.n.*, B100242419 (lecto B, here selected; isolecto B, BM, BR, F, G 3 sheets, HAL, P, W), Peru, Huánuco, Chinchao ('in nemoribus versus Chinchao vicum').

Guatteria excelsa Poepp. ex Mart. (1841) 38, syn. nov.; R.E.Fr. (1939) 371, f. 9c, d. — Type: *Poeppig 139* (*1467*) (holo W; iso B, BM, F, G, HAL, P), Peru, Huánuco, Pampayacu ('in submontanen Wäldern bei Pampayaco'), Oct. 1832.

Guatteria pilosula Triana & Planch. (1862) 31, syn. nov.; R.E.Fr. (1939) 369. — Type: *Linden 767* (holo P; iso BR, G), Colombia, Santander ('Las Lajitas, entre Pie de Cuesta et los Santos, prov. del Socorro'), 1300 m, Nov. 1842.

Guatteria cestrifolia Triana & Planch. (1862) 32; R.E.Fr. (1939) 366, f. 9a, syn. nov. — Type: *Triana s.n.* (holo P; iso BM, F, G, K, P, S, fragment), Colombia, Meta, Apiay ('Prov. de Bogotá, basin du Meta, Apiai'), 300 m.

Guatteria laurina Triana & Planch. (1862) 32; R.E.Fr. (1939) 366, t. 23, syn. nov. — Type: *Goudot s.n.* (holo P; iso K), Colombia, Meta, Irica ('haut Orénoque, pueblo de Iraca'), Dec. 1844.

Guatteria longipes Triana & Planch. (1862) 32; R.E.Fr. (1939) 516, t. 35, syn. nov. — Type: *Triana s.n.* (holo P; iso BM, COL, F, G, K), Colombia, Cundinamarca ('Prov. de Bogotá, Biota, Andes de Bogotá'), 2000 m, Sept. 1853.

Guatteria persicifolia Triana & Planch. (1862) 33, non J.D.Hook. & Thomson 1855; R.E.Fr. (1939) 367, syn. nov. — Type: *Schlim 700* (holo P; iso BM, BR 2 sheets, G 2 sheets, P), Colombia, Norte de Santander, Enllanada, 1200 m ('prov. de Ocaña, Enllanada, 3500 ped., June 1846–1852').

Guatteria alutacea Diels (1905) 126, syn. nov. — Type: *Ule 6427* (holo B; iso F, G, K, L, MG), Peru, San Martín, Tarapoto, Oct. 1902.

Guatteria juruensis Diels (1905) 126, syn. nov. — Type: *Ule 5010* (holo B; iso F, G, K, L, MG, S), Brazil, Amazonas, Rio Juruá, Marary, Sept. 1900.

Guatteria augusti Diels (1924a) 51, syn. nov. — Type: *Weberbauer 7062* (holo B; iso F, S, US), Peru, La Libertad, Prov. Patáz, Río Mixiollo, left branch of Río Huallaga, below Ongón, 1200–1300 m, 7 Aug. 1914.

Guatteria guentheriana Diels (1931) 75; R.E.Fr. (1939) 361, syn. nov. — Type: *Buchtien 1773* (holo B 2 sheets; iso F, NY, US), Bolivia, La Paz, Mapiri Region, San Carlos, 850 m, 2 May 1927.

Guatteria alutacea Diels var. *angustifolia* R.E.Fr. (1938) 710, syn. nov. — *Guatteria alutacea* Diels f. *angustifolia* (R.E.Fr.) R.E.Fr. (1939) 362. — Type: *Spruce 4270a* (holo B; iso BM, BR, E, G, K, NY, P, S, W), Peru, San Martín, Tarapoto, 1855–1856.

Guatteria klugii R.E.Fr. (1938) 710, syn. nov. — Type: *Klug 3299* (holo S; iso F, G, K, MO, NY, S, US), Peru, San Martín, Zepalacio, near Moyobamba, 1100–1200 m, Oct.–Nov. 1933.

Guatteria brevipedicellata R.E.Fr. (1939) 359, syn. nov. — Type: *Lawrance 771* (holo S; iso E, F 2 sheets, G, K 2 sheets, MO, US 2 sheets), Colombia, Boyacá, El Humbo, high forested fronts, 1250 m, 27 Apr. 1933.

Guatteria alutacea Diels var. *steinbachii* R.E.Fr. (1939) 362, syn. nov. — Type: *Steinbach 6486* (holo S; iso BM, E, F, G, K, MO, NY, PH), Bolivia, Santa Cruz, prov. Sara, Buenavista, 450 m, 27 Sept. 1924.

Guatteria ecuadorensis R.E.Fr. (1939) 364, syn. nov. — Type: *Mexia 7111* (holo S; iso F, K, NY, US), Ecuador, Napo, Zatzayacu, 400–500 m, 22 Mar. 1935.

Guatteria melinii R.E.Fr. (1939) 364, f. 26d, e, syn. nov. — Type: *Melin 122* (holo S), Peru, San Martín, San Roque, SE of Moyobamba, 9 May 1925.

Guatteria jamundensis R.E.Fr. (1939) 365, f. 8b, syn. nov. — Type: *Ducke MG 11780* = *RB 35322* (holo S; iso RB, S), Brazil, Pará, Lower Rio Jamundá, 18 May 1911.

Guatteria latisepala R.E.Fr. (1939) 368, syn. nov. — Type: *Lehmann K 27* (holo S; iso F, GH, K), Colombia, Cauca, Popayán, El Hatico, 1500–1800 m, 20 Mar. 1905.

Guatteria curvipetala R.E.Fr. (1939) 526, f. 36a, b, syn. nov. — Type: *Krukoff 6600* (holo S; iso BM, BR, F, G, K, MO, NY, RB 2 sheets, U, US), Brazil, Amazonas, Basin of Rio Madeira, Mun. Humaitá, Livramento, on Rio Livramento, 12 Oct. 1934.

Guatteria metensis R.E.Fr. (1948b) 6, pl. 2 a, b, syn. nov. — Type: *Haught 2470* (holo S 2 sheets; iso COAH, COL, NY, S, US 2 sheets), Colombia, Meta, Llanos and along Río Ocoa, 400 m, 19 Dec. 1938.

Guatteria chocoensis R.E.Fr. (1950a) 333, syn. nov. — Type: *Cuatrecasas 16592* (holo S 2 sheets; iso COL, F, US), Colombia, Valle del Cauca, Río Calima (región del Chocó), La Trojita, 5–50 m, 29 Feb. 1944.

Guatteria sp. 13 Chatrou et al. (1997) 111.

Tree or rarely a shrub 2.5–30(–42) m tall, 5–60 cm diam; young twigs densely to sparsely covered with erect to appressed, brown hairs 1.5–2 mm long, soon glabrous or long-persisting. *Leaves*: petiole 2–5(–10) mm long, 0.5–2 mm diam; lamina narrowly elliptic to narrowly oblong-elliptic, sometimes narrowly obovate, 7–22 by 1.5–6 cm (leaf index (2.3–)3.3–4.8(–8)), chartaceous, not verruculose, shiny or dull above, greyish, greyish black to brown above, brown to greyish brown, rarely greenish below, sparsely covered with erect to half-appressed hairs to glabrous above, the primary vein to densely so, becoming glabrous with age, densely to sparsely covered with erect to appressed hairs 1–2 mm long, primary vein to densely so below, becoming glabrous or almost so with age, base acute to obtuse, rarely cordate or attenuate, apex acuminate (acumen 5–20 mm long), primary vein flat, impressed or slightly raised above, secondary veins distinct, 8–15 on either side of primary vein, raised or sometimes impressed above, smallest distance between loops and margin 1–3 mm, tertiary veins raised above, reticulate. *Flowers* in 1(–3)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–40(–80) mm long, 1–1.5 mm diam, fruiting pedicels 2–3 mm diam, densely to sparsely covered with erect to appressed, brown hairs, articulated at 0.2–0.5 from the base, with the part above the articulation sometimes thicker than the part below, bracts 5–7, soon falling, basal ones broadly elliptic to elliptic, 1–2 mm long, the 2 upper ones and sometimes also a third bract below them elliptic to broadly elliptic, 4–10 mm long, occasionally foliaceous, to c. 45 mm long; flower buds depressed ovoid, pointed; sepals free, broadly ovate-triangular, 3–12 by 3–9 mm, appressed, finally reflexed, outer side densely to sparsely covered with erect or appressed hairs; petals green, maturing yellowish green, yellow, or white in vivo, ovate to obovate or narrowly so, 8–35 by 3–15 mm, outer side densely covered with appressed or erect hairs, particularly at the base; stamens 1–1.5 mm long, connective shield papillate to glabrous. *Monocarps* 10–100, green, maturing purplish to black in vivo, black in sicco, ellipsoid, 8–13 by 3–7 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum 0.1–2 mm long), wall 0.1–0.3 mm thick, stipes 8–25 by 0.5–1 mm. *Seed* ellipsoid, 6–10 by 3–6 mm, dark, shiny brown, pitted, sometimes also transversely grooved, raphe raised.

Distribution — Colombia (Amazonas, Antioquia, Cauca, Chocó, Huila, Meta, Norte de Santander, Santander, Valle del Cauca), Venezuela (Apure, Barinas, Falcón, Lara, Merida, Portuguesa, Táchira, Trujillo, Zulia), Ecuador (Azuay, Morona-Santiago, Napo, Pastaza, Zamora-Chinchipe), Peru (Amazonas, Cajamarca, Loreto, Madre de Dios, Pasco, Puno, San Martín), Brazil (Acre, Amazonas, Pará), Bolivia (Beni, Cochabamba, La Paz, Santa Cruz).

Habitat & Ecology — In non-inundated, rarely periodically inundated (várzea) lowland, montane or submontane forest, sometimes in savannas, on sandy to limestone soil. At elevations of 0–2000(–2400) m. Flowering: throughout the year; fruiting: August to April.

Vernacular names — Bolivia: Negrillo (*Steinbach 6486*), Piraquina macho (*Zonta et al. 104*), Piraquina negra (*Arrazola 16*, *Del Aguila et al. 364*, *Meneces & Zabala 356*, *Moraes R. 940*, *Zabala & Terceros s.n.*). Brazil: Envira-caju (*Daly et al. 8325*), Envira-tambaqui (*Sothers & Araujo 18*). Colombia: Anona de monte (*Little 8731*), Cargadero (*Cuatrecasas 16592*), Garrapato (*Cárdenas L. & Ramirez 2654*, *Zarucchi 3378*), Suta (*Lawrance 771*). Peru: Carahuasca (*Croat 19216*, *Vásquez 6686*, *Vásquez & Jaramillo 10321*), Espintana (*J. Ruíz & Murphy 276*). Venezuela: Laurel (*Veillon 85*), Magua negra (*Breteler 3922*).

Field observations — *Nee 37977* (U) from Bolivia has 'spicy fragrant flowers'. *Amaral et al. 457* (U) from Brazil has immature fruits emitting a scent of ripe bananas ('frutos imaturos exalando cheiro de banana madura').

Notes — The main features of *G. hirsuta*, belonging to sect. *Trichoclonia*, are narrow, often greyish black coloured leaves, an indument of erect to appressed, brown hairs on the leafy twigs, relatively long pedicels and pitted seeds.

Fig. 43 *Guatteria hirsuta* Ruiz & Pav. Flowering branch (*Nee 37977*, U).

We decided to unite here four species described by Triana and Planchon in the same paper (1862). These species differ from each other only in minor aspects (among others, leaf base, leaf indument, shape of petals), but examination of more specimens than must have been at the disposal of Triana and Planchon makes obvious that there are many intergradations.

It is with some reluctance that we united *G. latisepala* with *G. hirsuta*. *Guatteria latisepala* is found mostly at higher elevations (c. 800 m and up), and many specimens look quite distinct by a more dense indument and by markedly thickened pedicels above the articulation point. There are too many transitional forms, though, to justify keeping the two species apart.

Guatteria alutacea as described at first seems well distinct by the greyish to greyish black colour of the upper side of the leaves, the mostly obtuse to acute leaf base, and often the presence of rather long appressed and forward-pointing hairs on the lower side of the lamina. However, there are also many intergradations here that make it impossible to uphold *G. alutacea* as a separate species.

Forms described as *G. alutacea* var. *angustifolia* are noticeable because of very narrow and attenuate leaves with a leaf index up to 8 and generally long pedicels, but otherwise are not clearly distinct.

Guatteria longipes, known only from the type collected in the Colombian state of Cundinamarca ('Prov. de Bogotá, Biota, Andes de Bogotá'), at an elevation of 2000 m, differs by pedicels 50–90(–120) mm long!

Some forms, all from the Colombian state of Chocó, are noteworthy because of their tendency towards longer-than-average pedicels: *Cuatrecasas & Llano 24070* (to 80 mm long!), *Gentry et al. 17844* and *30242.* Apart from that, they match well with the overall description.

81. *Guatteria hispida* (R.E.Fr.) Erkens & Maas — Map 18

Guatteria hispida (R.E.Fr.) Erkens & Maas (2008) 404; Maas & Westra (2011) 129, f. 13. — *Guatteriopsis hispida* R.E.Fr. (1934) 111, t. 7, 8; Maas et al. (2007) 645. — Type: *Ducke 14 = RB 23903* (holo S; iso K, RB, US), Brazil, Amazonas, Manaus, Estrada do Aleixo, km 12, 9 Dec. 1932.

Tree or shrub 2–6 m tall, c. 5 cm diam; young twigs densely covered with brown, rough, erect, long-persistent hairs ('hirsute') to c. 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 ('hirsute') below, base acute to obtuse, apex abruptly and long-acuminate (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, tertiary veins slightly raised above, reticulate. *Flowers* solitary in axils of leaves; flowering and fruiting pedicels 5–8 mm long, 3–5 mm diam, densely to finally sparsely covered with erect, brown hairs, articulated at c. 0.7 from the base, bracts 5–6, soon falling, the uppermost bract 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, hairs to c. 3 mm long; stamens c. 2 mm long, connective shield hairy. *Monocarps* 10–50, 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 ('hirsute'), apex distinctly and bluntly apiculate (apiculum < 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, longitudinally and transversely grooved to rugulose, raphe not distinct from rest of seed.

Distribution — Amazonian Brazil (Amazonas).

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

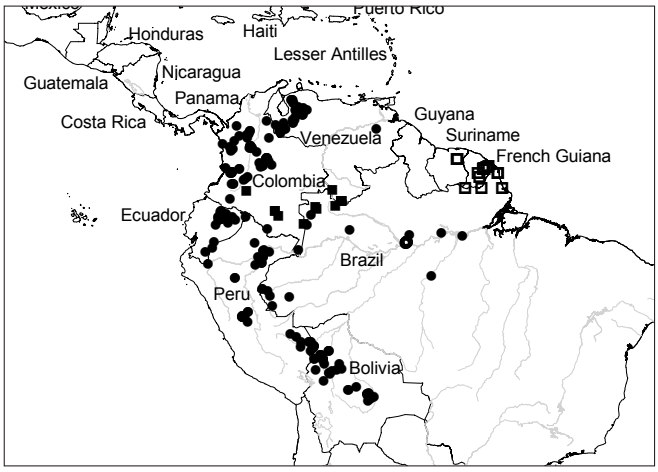
Vernacular name — Brazil: Envireira.

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

82. *Guatteria insculpta* R.E.Fr. — Map 18

Guatteria insculpta R.E.Fr. (1939) 504, f. 28a, b; Murillo A. & Restrepo (2000) 95, f. 25; Maas & Westra (2011) 131, f. 1c, 14, 15. — Type: *Spruce 2896* (holo K 2 sheets; iso BM, BR, P), Brazil, Amazonas, Ipanoré ('Panuré'), Rio Uaupés, 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, 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 forming a more or less distinct marginal vein, at a smallest distance of 3–4 mm from the margin, tertiary veins impressed above, percurrent. *Flowers* solitary in axils of leaves or on leafless branchlets; pedicels 18–40 mm long, 2–4 mm diam, fruiting pedicels to c. 50 mm long, c. 5 mm diam, densely covered with erect, red-brown hairs, articulated at 0.1–0.2 from the base, bracts soon falling, the upper bract to c. 7 mm long; flower buds not seen; sepals free, triangular to broadly ovate-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, maturing brown in vivo, pale brown in sicco, ellipsoid, 10–18 by 5–12 mm, sparsely covered with appressed hairs, apex rounded to 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 grooved, raphe not distinct from rest of seed.



Map 18 Distribution of *Guatteria hirsuta* (●), *G. hispida* (⭘), *G. insculpta* (■) and *G. intermedia* (□).

Distribution — Amazonian Colombia (Amazonas, Caquetá), Venezuela (Amazonas), 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 name) (*Murillo A. & Rodríguez 544*), Jimokai (Huitoto name), 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.

83. *Guatteria intermedia* Scharf — Map 18

Guatteria intermedia Scharf in Scharf et al. (2006b) 545, f. 2. — Type: *Oldeman B.4125* (holo CAY; iso NY), French Guiana, Saül, Crique Cochon, 21 Oct. 1971.

Tree 2–10 m tall, 5–15 cm diam; young twigs densely covered with semi-erect, brown, long-persisting hairs. *Leaves*: petiole 3–10 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly obovate, 10–23 by 4–7.5 cm (leaf index 2.6–3.4), chartaceous, not verruculose, dull greyish above, greyish brown to reddish brown below, sparsely covered with appressed, long hairs above, soon glabrous, primary vein with a row of semi-erect hairs, densely covered with appressed, pale brown hairs below, base acute, apex acuminate (acumen 10–20 mm long), primary vein impressed above, secondary veins distinct, 10–12 on either side of primary vein, flat to slightly raised above, smallest distance between loops and margin 1.5–3 mm, tertiary veins slightly raised above, percurrent to reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; flowering and fruiting pedicels 5–20 mm long, 1–2 mm diam, densely covered with semi-erect, brown hairs, articulated at 0.3–0.4 from the base, bracts 5–6, soon falling, not seen; flower buds depressed ovoid; sepals free or slightly connate at the base, broadly to shallowly ovate-triangular, 4–5 by 5–7 mm, apex reflexed, outer side densely covered with appressed hairs (apex glabrous); petals greenish yellow or yellow in vivo, narrowly oblong-elliptic to oblong-elliptic,10–20 by 5–10 mm, outer side densely covered with appressed to erect, rusty brown, curly hairs; stamens 1.5–2 mm long, connective shield papillate, rarely hairy, mostly umbonate. *Monocarps* 20–50, green, maturing black in vivo, shiny black or blackish brown in sicco, ellipsoid, 5–9 by 3–5 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 1 mm long), wall 0.1–0.2 mm thick, stipes 10–25 by 0.5–1 mm. *Seed* ellipsoid, 6–8 by 4–5 mm, shiny, dark brown, pitted, raphe not distinct from rest of seed.

Distribution — NW Suriname, French Guiana, Brazil (Amapá).

Habitat & Ecology — In non-inundated forest, on lateritic or sometimes on granitic soil. At elevations of 0–400 m. Flowering: June to March; fruiting: February, October to December.

Vernacular names — French Guiana: Iwi, I-wi (Wayãpi name) (*de Granville T.1151*, *Grenand 632*, *Prévost & Grenand 967*, *Prévost & Sabatier 2781*), Mamayavé (Creole name) (*de Granville B.4561*).

Notes — The recently described *G. intermedia* differs from *G. ouregou* and *G. richardii*, by having semi-erect to appressed instead of erect hairs on young twigs and pedicels.

Except for the indument, *G. intermedia* shares many features with *G. punctata.* To complicate matters, though, there are some specimens cited by Scharf (Scharf et al. 2006b) under *G. intermedia* which lack the indument of semi-erect hairs, having an indument of appressed hairs instead. This involves *Mori et al. 25705* from French Guiana, and *Van Andel et al. 4657* from Suriname. In almost all material of *G. punctata* studied by us we observed a very distinct indument of appressed hairs on most of the parts. In the Brazilian state of Mato Grosso, however, we came across some material with erect or almost erect hairs. These specimens had been identified as *G. sylvicola.* In that case, too, we found various specimens with an indument intermediate between that of *G. sylvicola* and that of 'typical' *G. punctata* making us conclude that all material should be referred to *G. punctata*. Possibly *G. intermedia* represents a similar case of a slightly deviating population within *G. punctata* in the wide sense.

84. *Guatteria inundata* Mart. — Plate 4h, i; Map 19

Guatteria inundata Mart. (1841) 36; R.E.Fr. (1939) 411, f. 14f, g, t. 28. — Type: *Martius s.n.* (lecto M, selected by Fries 1939), Brazil, Amazonas, Rio Solimões and Rio Japurá ('in inundatis ripae fluv. Solimões et Japurae'), 14 Dec. 1819.

Guatteria inundata Mart. var. *longifolia* Poepp. ex Mart. (1841) 36. — *Guatteria dolichophylla* R.E.Fr. (1939) 414, syn. nov. — Type: *Poeppig 2693* (holo BR; iso B, BM, F, G, HAL, P, W), Brazil, Amazonas, along a lake near Tefé ('in sylvis litoreis lacus Egensis'), Oct. 1831.

Guatteria phanerocampta Diels (1931) 76; R.E.Fr. (1939) 415. — Type: *Ll. Williams 3436* (syn F, G, S, US), Peru, Loreto, Upper Río Itaya, San Antonio, 145 m, 5 Oct. 1939.

Guatteria riparia R.E.Fr. (1939) 410; Steyerm. et al. (1995) 446, f. 377, syn. nov. — Type: *Spruce 3105* (holo K; iso BM, BR, C, G 3 sheets, NY, P), Venezuela, Amazonas, banks of Río Negro and Río Casiquiare, Oct. 1853.

Guatteria obovata R.E.Fr. (1939) 412, f. 14h; Morawetz (1984) 59, syn. nov. — Type: *R.H. Schomburgk I 922* (holo K; iso B, BM, E, F, FI 2 sheets, G 3 sheets, L, P, U, US, W), Brazil, Amazonas, Rio Negro, Lago Pedrero, 1840.

Guatteria oblanceolata R.E.Fr. (1939) 415. — Type: *Krukoff 6721* (holo S; iso BM, BR, F, G, K, MO, NY, RB, U, US 2 sheets), Brazil, Amazonas, Mun. Humaitá, near Livramento, on Rio Livramento, 12 Oct. to 6 Nov. 1934.

Many-stemmed shrub or sometimes a tree 1–10(–20) m tall, up to c. 10 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 5–15 mm long, 1–2 mm diam; lamina narrowly elliptic, 15–27 by 4–8 cm (leaf index 2.3–5.6), chartaceous, sometimes rugulose, brownish green, brown, to greyish green above, brown to greenish brown below, glabrous above, sparsely covered with appressed hairs below, base attenuate, apex acuminate (acumen 10–20 mm long) to long-acute, primary vein impressed above, secondary veins distinct, 12–20 on either side of primary vein, impressed to slightly raised above, smallest distance between loops and margin 2–6 mm, tertiary veins flat to slightly raised above, reticulate. *Flowers* solitary in leaf axils, rarely on leafless branchlets; pedicels 12–40 mm long, 1–1.5 mm diam, fruiting pedicels to c. 50 mm long, c. 2 mm diam, sparsely covered with appressed hairs, articulated at 0.2–0.6 from the base, bracts 4–6, soon falling, broadly triangular-elliptic, broadly ovate, or elliptic, 1.5–6 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–6 by 4–6 mm, appressed, outer side densely to rather densely covered with appressed hairs; petals green, maturing cream or yellow in vivo, ovate to obovate, 15–35 by 8–20 mm, outer base densely covered with appressed hairs, apical part rather densely to sparsely so; stamens c. 2 mm long, connective shield papillate to glabrous. *Monocarps* 25–50, green, maturing reddish in vivo, black, rarely brownish in sicco, narrowly ellipsoid and mostly fusiform, 17–30 by 5–7 mm, sparsely covered with appressed hairs, soon glabrous, apex distinctly apiculate and hard-pointed (apiculum 1–3 mm long), wall 0.1–0.3 mm thick, stipes 2–5 by 1–2 mm. *Seed* narrowly ellipsoid, 15–25 by 5–8 mm, pale brown, pitted, longitudinally grooved, with spongy appearance, raphe not distinct from rest of seed.

Distribution — Amazonian Colombia (Vaupés), Venezuela (Amazonas), Peru (Loreto), Brazil (Amazonas, Pará, Roraima).

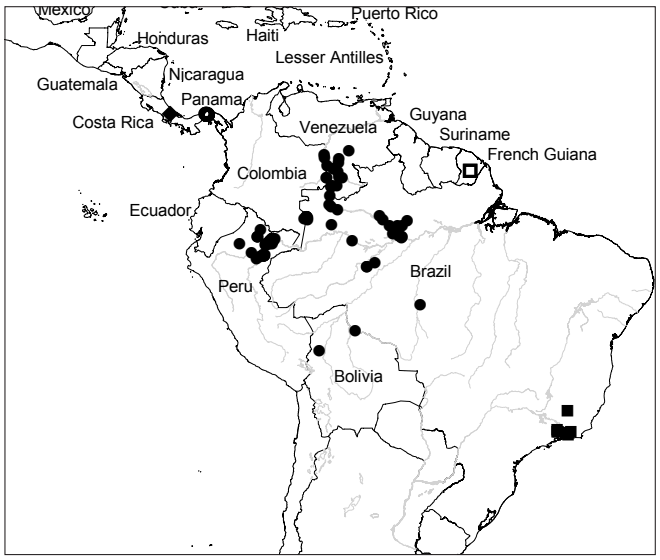
Habitat & Ecology — Mostly in periodically inundated forest (igapó, várzea or tahuampa), on clayey to sandy soil. At elevations of 0–200 m. Flowering: throughout the year, but mostly between September and November; fruiting: November to June.

Vernacular names — Brazil: Cacaia-velha (*Zappi et al. 2967*), Envira-do-igapó (*Albuquerque & Lima 227*). Peru: Anona (*McDaniel & Rimachi Y. 17539*, *Rimachi Y. 2443*, *2557*), Anonilla (*Rimachi Y. 12305*), Bara (*Rimachi Y. 907*, *2706*, *6447*), Bar(r)a caspi (*McDaniel & Rimachi Y. 20386*, *Rimachi Y. 1840*), Carahuasca (*Del Carpio & Ruiz 1606*), Espintana (*Peters 22*, *Rimachi Y. 1809*, *10719*), Motelo caspi (*Rimachi Y. 3348*). Venezuela: Kunwata (*L. Delgado et al. 953*), Majagua (*Breteler 4844*, *Stergios & Aymard C. 9010*), Majagua negra (*Liesner 6233*), Majagua orillera (*Liesner 6501*), Majagua rebalsera (*Delgado 593*), Palo de boya negro (*Ll. Williams 14727*).

Notes — *Guatteria inundata* is a species quite often collected in periodically inundated várzea, tahuampa and igapó forests of Amazonian Brazil, Peru and Venezuela. It is most easy to recognize by the long-apiculate and almost pointed monocarps, very rarely met with in the genus. The seeds of this species have a spongy outer layer which may be an adaptaton to hydrochory (the species is restricted to river banks!). Fries (1939) placed *G. inundata*, *G. dolichophylla*, *G. oblanceolata*, *G. obovata*, *G. phanerocampta* and *G. riparia* in sect. *Stenocarpus*. In his key to the 6 species he used characters such as leaf shape, secondary veins and leaf colour. In the initial phase of our study we only recognized a mere two species, viz. *G. inundata* and *G. riparia*, with as main differentiating characters the leaf shape, leaf apex and distance between loops and the margin. With the steady increase of many new collections these differences gradually became blurred, leaving us no other option but to unite all in *G. inundata*.

In most collections studied the monocarps are very narrow and almost fusiform, but in a few collections the monocarps are much broader and the apex even obtuse.

One collection, *Glaziou 13505* (P: 'Brazil, Rio de Janeiro, Morro do Cocco, 9 February 1882'), falls quite far out of the distribution range of this typically Amazonian species. A similar case is that of *Glaziou 13504* (see under *G. foliosa*). As Glaziou quite often used erroneous data (see Wurdack 1970) we have the suspicion that the locality data are incorrect.



Map 19 Distribution of *Guatteria inundata* (●), *G. jefensis* (⊙), *G. latifolia* (■), *G. leucotricha* (□) and *G. pachycarpa* (◆).

85. *Guatteria japurensis* Maas & Westra — Map 20

Guatteria japurensis Maas & Westra in Erkens et al. (2008) 497, f. 12; Maas & Westra (2011) 131. — Type: *Amaral et al. 518* (holo U; iso INPA, NY, RB), Brazil, Amazonas, right bank of Rio Japurá, Villa 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 (index 3–4), chartaceous to thinly coriaceous, scabridulous above, not or sparsely verruculose along primary vein only, slightly shiny and brownish green above, dull brownish green below, glabrous on both sides, base obtuse, extreme 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, tertiary veins flat to slightly raised above, reticulate. *Flowers* in 1–several-flowered inflorescences in axils of leaves or on leafless 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, bracts 5–6, soon falling, not seen; flower buds, sepals, petals and stamens not seen. *Monocarps* 10–15, immature, colour not recorded in vivo, 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, longitudinally and transversely grooved, raphe not distinct from rest of seed.

Distribution — Western Amazonian Brazil (Amazonas).

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

Vernacular names — Not recorded.

Note — *Guatteria japurensis* is most distinctive by the long and slender fruiting pedicels bearing rather long monocarps, a combination very uncommon in *Guatteria*. Another noteworthy feature is found in the leaves which are indistinctly veined and are scabridulous on the upper surface.

86. *Guatteria jefensis* Barringer — Plate 5a, b; Map 19

Guatteria jefensis Barringer (1984) 1186. — Type: *Hammel 6302* (holo MO), Panama, Panamá, Cerro Jefe near radio tower, in Clusia forest, 1000 m, 3 Mar. 1979.

Tree or shrub 1–6 m tall, 2–5 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 3–8 mm long, 1–3 mm diam; lamina narrowly ovate to elliptic, 7–20 by 3–7 cm (leaf index 2.3–3), coriaceous, often folded lengthwise when dry, not verruculose, dull, greyish green above, brown below, sparsely covered with erect hairs along primary vein and secondary veins above, sparsely covered with appressed hairs below, base obtuse, apex acuminate (acumen to c. 10 mm long), primary vein impressed above, secondary veins distinct, 10–13 on either side of primary vein, impressed to flat above, smallest distance between loops and margin 3–4 mm, tertiary veins flat above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–50 mm long, 1–3 mm diam, fruiting pedicels 30–50 mm long, 3–4 mm diam, densely covered with appressed hairs, articulated at c. 0.2 from the base, bracts 5–7, gradually increasing in size from basal to c. 2 mm long to uppermost to c. 5 mm long, occasionally foliaceous, elliptic, 20–30 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 5–8 by 5–7 mm, appressed, finally becoming spreading to slightly reflexed, margins revolute, outer side densely covered with appressed hairs; petals yellowish green

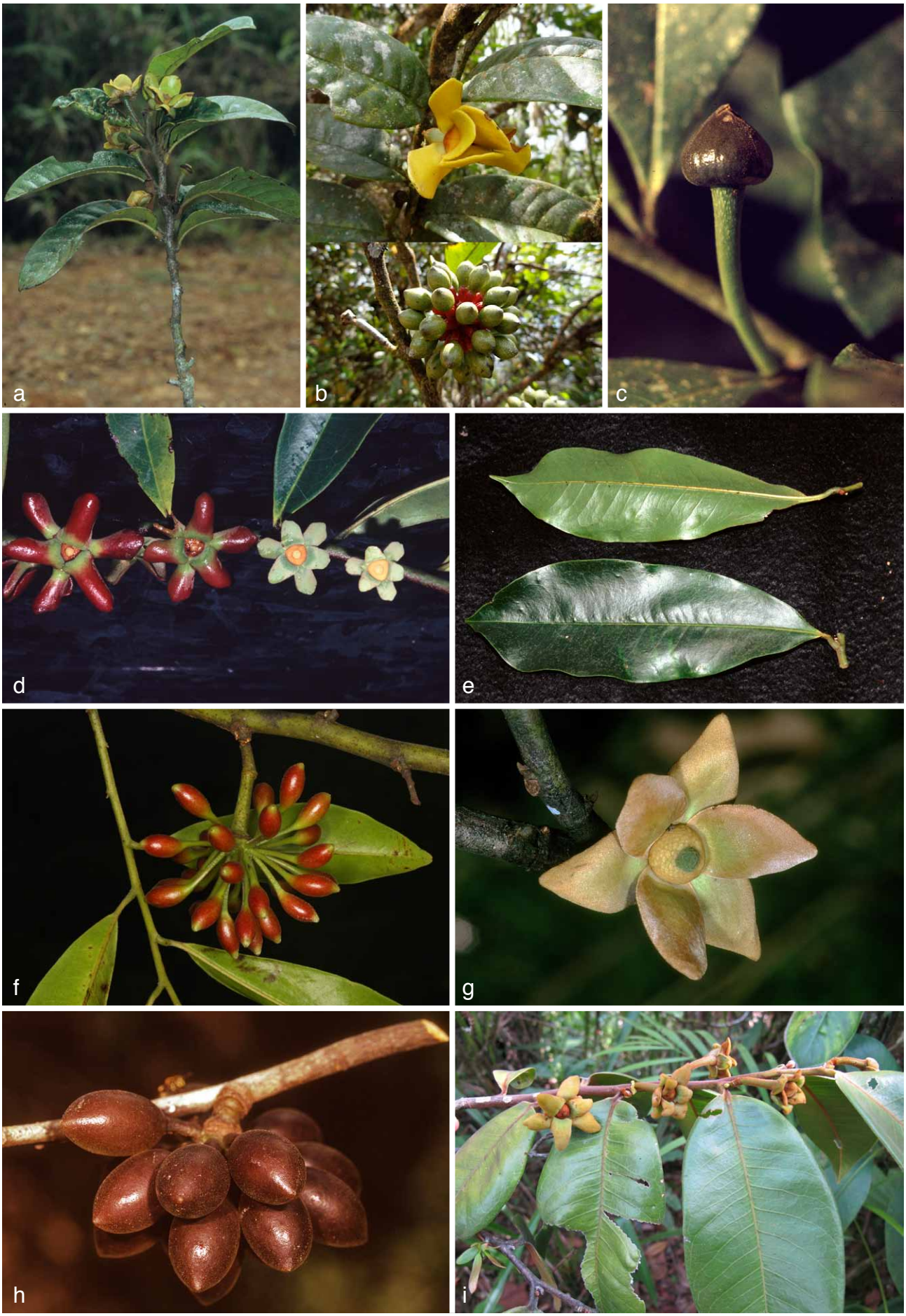
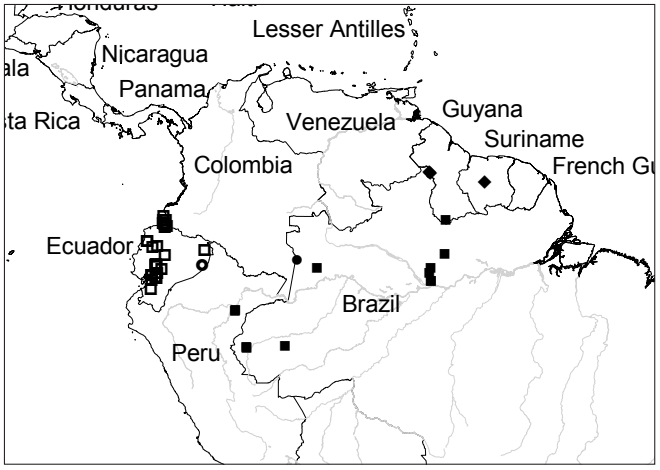


Plate 5 a, b. *Guatteria jefensis* Barringer. a. Flowering branch of dwarf tree; b. ripe flower (top), fruit (bottom). – c. *Guatteria latifolia* (Mart.) R.E.Fr. Flower bud. – d–f. *Guatteria lucens* Standl. d. Flowers; e. leaves; f. fruit. – g, h. *Guatteria megalophylla* Diels. – g. Flower; h. fruit. – i. *Guatteria oblongifolia* Rusby. Flowering branch (a: *Maas et al. 9553*; b: Cerro Jefe, Panama; c: *Maas & Martinelli 3222*; d; *Maas et al. 9491*; e: *Maas et al. 9519*; f: *Chatrou et al. 705*; g, h: *Chatrou et al. 387*; i: *Homeier 4504*). — Photos: a, c–e: P.J.M. Maas; b: J. Harrison; f–h: L.W. Chatrou; i: J. Homeier.



Map 20 Distribution of *Guatteria japurensis* (●), *G. megalocarpa* (⭘), *G. meliodora* (■), *G. microcarpa* (□) and *G. minutiflora* (◆).

or yellow in vivo, broadly ovate to obovate, 10–15{–20} by 7–15 mm, outer side densely covered with appressed hairs; stamens 1–2 mm long, connective shield glabrous, sometimes slightly umbonate. *Monocarps* 25–50, green, maturing blackish purple in vivo, black in sicco, ellipsoid, 10–13 by 5–7 mm, glabrous, apex rounded to apiculate (apiculum nipple-shaped, to c. 1 mm long), wall 0.2–0.3 mm thick, stipes 4–8 by 1–2 mm, distinctly constricted at the apex. *Seed* ellipsoid, 8–11 by 5–6 mm, dark brown, pitted, raphe not distinct from rest of seed.

Distribution — Panama.

Habitat & Ecology — In dwarf cloud forest. At elevations of 800–1000 m. Flowering: January to June, September, November; fruiting: January to April, October, December.

Vernacular names — Not recorded.

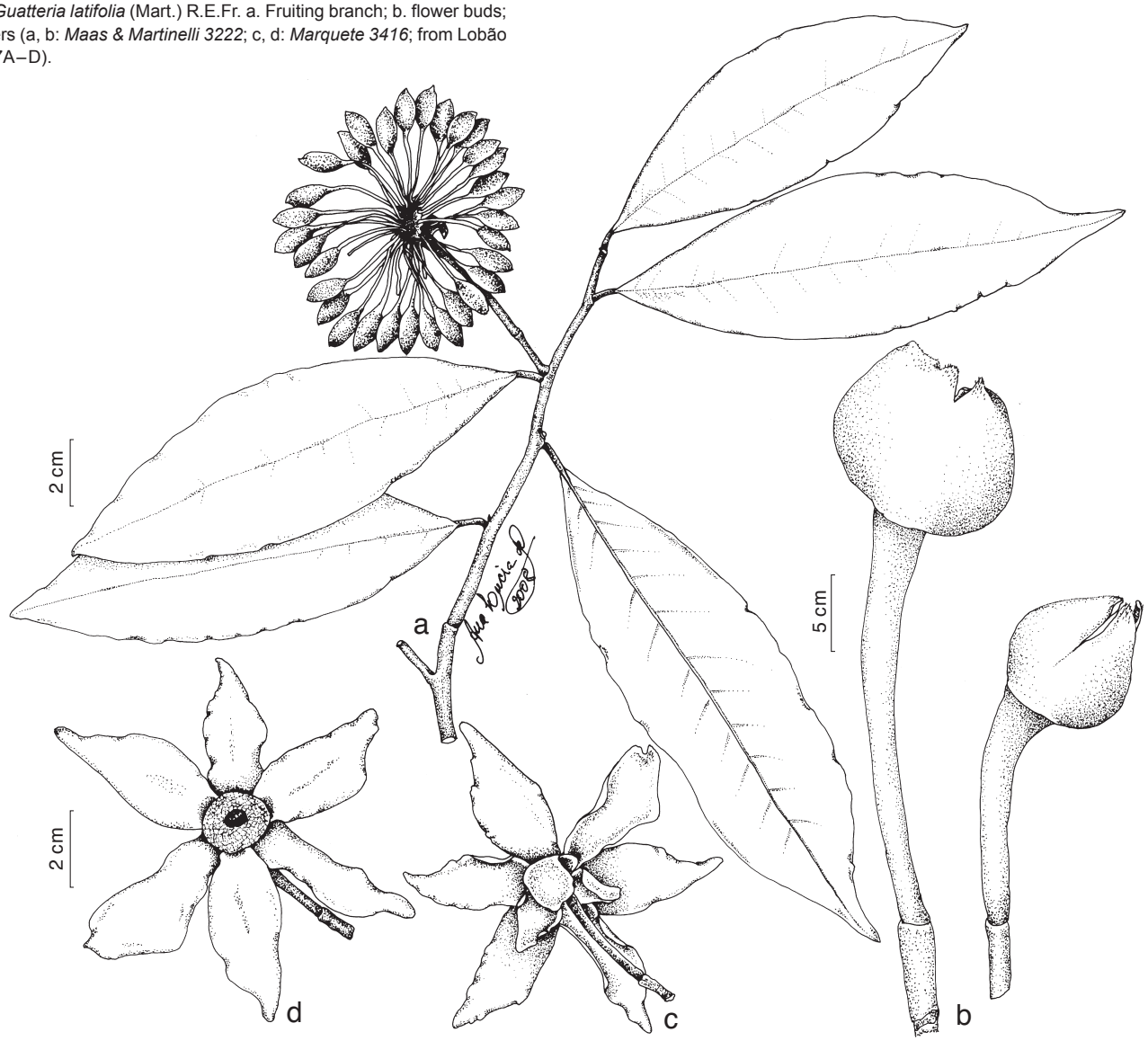
Note — *Guatteria jefensis*, one of the many narrow endemics of Cerro Jefe, is easily distinguished by its thick, often lengthwise folded leaves and by its constricted stipes.

87. *Guatteria latifolia* (Mart.) R.E.Fr. — Fig. 44; Plate 5c; Map 19

Guatteria latifolia (Mart.) R.E.Fr. (1939) 326, f. 4a. — *Guatteria nigrescens* Mart. var. *latifolia* Mart. (1841) 31. — *Type*: *Schott s.n.* (holo BR), Brazil, Rio de Janeiro, Serra do Tinguá.

Tree or shrub 4–10 m tall, 6–20 cm diam; young twigs glabrous. *Leaves*: petiole 5–8 mm long, c. 2 mm diam; lamina narrowly elliptic to elliptic, 10–20 by 3–7 cm (leaf index 2–4), chartaceous, not verruculose, shiny, blackish green to brown above, pale brown below, glabrous above, sparsely covered with appressed, brown hairs to glabrous below, base acute, apex acute to acuminate (acumen c. 10 mm long), primary vein impressed above, secondary veins distinct, 10–12 on either side of primary vein, raised to impressed above, smallest distance between

Fig. 44 *Guatteria latifolia* (Mart.) R.E.Fr. a. Fruiting branch; b. flower buds; c, d. flowers (a, b: *Maas & Martinelli 3222*; c, d: *Marquete 3416*; from Lobão (2009) f. 7A–D).



loops and margin c. 1 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 25–45(–60) mm long, 1–3 mm diam, fruiting pedicels to c. 70 mm long, sparsely covered with appressed, brown hairs to glabrous, articulated at < 0.1 from the base, bracts 2, soon falling, c. 10 by 2 mm; flower buds broadly ovoid; sepals connate, broadly ovate-triangular to ovate-triangular, 10–20 by 10 mm, reflexed, outer side sparsely covered with erect, curly, brown hairs; petals cream or yellow in vivo, narrowly elliptic to elliptic, 15–35 by 6–20 mm, outer side sparsely covered with erect, curly, brown hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* 15–45, purple in vivo, black in sicco, ellipsoid, 6–15 by 5–7 mm, glabrous, apex apiculate (apiculum c. 1 mm long), wall 0.2–0.5 mm thick, stipes 20–30 by 1 mm. *Seed* ellipsoid to subglobose, 6–15 by 5–7 mm, brown to dark brown, pitted, raphe not distinct from rest of seed.

Distribution — Brazil (Minas Gerais, Rio de Janeiro).

Habitat & Ecology — In non-inundated, Atlantic rain forest, on clayey soil. At elevations of 150–1250 m. Flowering: August to March; fruiting: January to March, June, September, November.

Vernacular name — Brazil: Canguantã (*M.R. Barbosa 261*, *Fernandes 399*).

Note — Large flower buds and connate sepals are striking aspects of *G. latifolia*.

88. *Guatteria leucotricha* Scharf & Maas — Map 19

Guatteria leucotricha Scharf & Maas in Scharf et al. (2006a) 123, f. 3. — Type: *Mori & Boom 15360* (holo NY; iso CAY, K, P, U, US), French Guiana, Saül, along road to airport, 200–400 m, 8 Dec. 1982.
Guatteria spec. A Maas & Maas-van de Kamer (2002) 62.

Tree 20–30 m tall, 35–45 cm diam, with steep, simple, round buttresses; young twigs densely covered with appressed hairs to c. 0.5 mm long, soon glabrous. *Leaves*: petiole 4–5 mm long, 1–1.5 mm diam; lamina narrowly elliptic to narrowly obovate, 9–14 by 2–3 cm (leaf index 3.5–4.5), chartaceous to subcoriaceous, not verruculose, dull, greyish green to brown above, brown below, densely covered with appressed, silvery, long hairs above, very soon glabrous, densely covered with appressed, silvery hairs below, base long-attenuate, apex acuminate (acumen 10–15 mm long), margins recurved, primary vein impressed above, secondary veins indistinct, 8–13 on either side of primary vein, slightly raised to flat above, indistinctly loop-forming, smallest distance between loops and margin 1–2 mm, tertiary veins slightly raised above, reticulate. *Flowers* solitary on leafless branchlets; flowering pedicels not seen, fruiting pedicels 5–10 mm long, 1–1.5 mm diam, sparsely covered with appressed, whitish hairs, articulated at 0.3–0.4 from the base, bracts c. 6, soon falling, not seen; flower buds, sepals, petals and stamens not seen. *Monocarps* 5–20, maturing dark purple in vivo, shiny black in sicco, ellipsoid to obovoid, 7–9 by 5–7 mm, somewhat wrinkled in sicco, sparsely covered with appressed, whitish hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.3–0.5 mm thick, stipes 10–13 by c. 1 mm. *Seed* ellipsoid, 5–7 by 3–4 mm, shiny, red-brown, rugulose, raphe raised.

Distribution — Central French Guiana.

Habitat & Ecology — In non-inundated, moist forest. At elevations of 200–400 m. Flowering: unknown; fruiting: September, December.

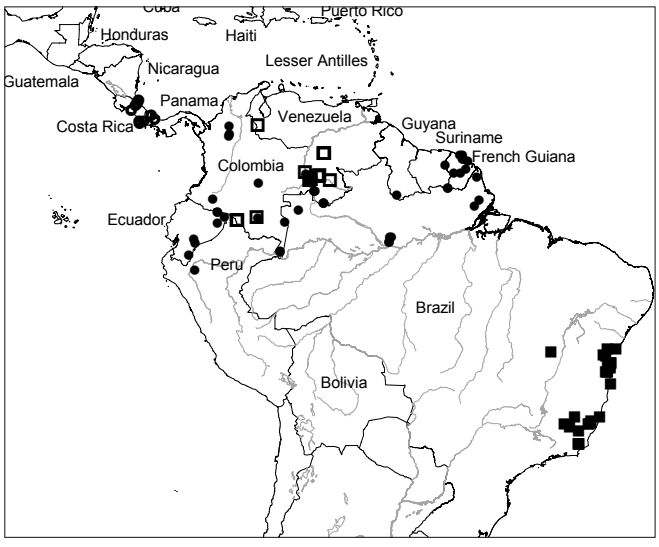
Vernacular names — Not recorded.

Note — *Guatteria leucotricha* is very well characterized by long-attenuate leaves with recurved margins and by a dense indument of appressed silvery hairs on the lower side of the lamina. It comes very close to the allopatric *G. modesta*, which is known from Amazonian Colombia, Ecuador and Peru. *Guatteria modesta*, however, lacks the silvery indument on the lower side of the lamina and the seeds are very different (pitted in *G. modesta* and rugulose in *G. leucotricha*).

89. *Guatteria liesneri* D.M.Johnson & N.A.Murray — Map 21

Guatteria liesneri D.M.Johnson & N.A.Murray (1990) 598; Steyerm. et al. (1995) 446; Murillo A. & Restrepo (2000) 101, f. 28. — Type: *Nee 30864a* (holo NY; iso F, MO, U, US, VEN), Venezuela, Amazonas, Dep. Río Negro, along Río Baria (= Río Mawarinuma), just upstream from base camp, SW side of Cerro Neblina, 140 m, 15 Feb. 1985.
Guatteria anthracina Scharf & Maas in Scharf et al. (2006a) 118, f. 1; Maas et al. (2007) 642, syn. nov. — Type: *Lindeman*, *Stoffers et al. 429* (holo U; iso BBS, F, K, MO, NY, U, VEN), Suriname, Lely Mts, 550–710 m, 26 Nov. 1975.
Guatteria aff. *oblonga* sensu Maas & Maas-van de Kamer (2002) 62, not R.E.Fr.

Tree 3–30 m tall, 2–45 cm diam; young twigs sparsely covered with appressed or very rarely erect hairs, soon glabrous. *Leaves*: petiole 3–7 mm long, 1–2 mm diam; lamina narrowly oblong-elliptic to narrowly ovate, rarely narrowly obovate, 7–22 by 2–8 cm (leaf index 2.4–5), chartaceous, not verruculose, shiny to dull above, black to dark brown above, brown to blackish brown below, sparsely covered with appressed hairs to glabrous above, primary vein densely covered with erect hairs to glabrous, sparsely to rather densely covered with appressed hairs to glabrous below, base obtuse, acute or attenuate, apex acuminate (acumen 5–35 mm long), primary vein slightly impressed or flat above, secondary veins distinct, 7–20 on either side of primary vein (sometimes seemingly more due to large intersecondaries), strongly to slightly raised above, smallest distance between loops and margin 2–5 mm, tertiary venation raised above, mostly reticulate. *Flowers* in 1–2(–3)-flowered inflorescences in axils of leaves or sometimes on leafless branchlets; pedicels 10–25 mm long, c. 1 mm diam, fruiting pedicels to c. 35 mm long, 1.5–2 mm diam, densely to sparsely covered with appressed or rarely erect hairs, articulated at 0.2–0.3 from the base, bracts 5–7, soon falling, broadly elliptic to narrowly obovate-elliptic, basal bracts broadly ovate, 1–2 mm long, upper ones to c. 6 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–6 by 3–5 mm, reflexed, outer side densely to sparsely covered with appressed hairs; petals green, maturing yellowish green, yellow or cream in vivo, elliptic to obovate or narrowly so, 12–30 by 5–13 mm, outer side densely covered with appressed hairs; stamens 1–1.5 mm long, connective shield papillate, sometimes slightly umbonate.



Map 21 Distribution of *Guatteria liesneri* (●), *G. lucens* (⭘), *G. macropus* (■) and *G. maguirei* (□).

Monocarps 20–60, green, maturing yellow, red to finally black in vivo, black to dark reddish brown in sicco, ellipsoid, 8–11 by 4–5 mm, densely covered with appressed hairs when young, soon glabrous, apex apiculate (apiculum 0.5–1 mm long), wall 0.1–0.2 mm thick, stipes 10–25 by 0.5–1 mm. *Seed* ellipsoid, 3–10 by 4–6 mm, pale to dark brown, pitted to transversely grooved, raphe not distinct from rest of seed.

Distribution — Colombia (Amazonas, Antioquia, Guainía, Putumayo, Vaupés), Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana, Amazonian Ecuador (Morona-Santiago, Napo, Sucumbios), Peru (Amazonas, San Martín), Brazil (Amapá, Amazonas, Pará).

Habitat & Ecology — In non-inundated or rarely periodically inundated lowland forest, but also in premontane or montane forest, on clayey to sandy soil. At elevations of 100–2000 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Brazil: Envira (*L.F. Coêlho INPA 6363*). Colombia: Garapato (*Zarucchi 3378*), Jïrïda (Huitoto name) (*Vester & Castro 144*), Naqueno (*Betancur B. et al. 5298*), Pitaruguï (Tukano name), (*Urrego B. et al. 1013*). Ecuador: Uñitahue (Huaorani name) (*M. Aulestia & Bainca 3551*).

Notes — *Guatteria liesneri* is generally easy to recognize by its blackish to dark brown leaves, with mostly a strongly raised tertiary venation. From *G. foliosa* it differs by often blackish leaves, smaller petioles (3–7 by 1–2 vs 5–15 by 0.5–1 mm) and pitted to transversely grooved instead of smooth seeds.

Guatteria anthracina is united here with *G. liesneri* as the differences mentioned by Scharf et al. (2006a) including leaf and petiole size, and an acute rather than attenuate leaf base, appeared not to stand up after many intermediate forms turned up with examination of more material.

Material from Antioquia, Colombia, is slightly aberrant in having pedicels that are covered with erect instead of appressed hairs.

McPherson et al. 13430 (U) from Antioquia, Colombia and *Rangel et al. 12494* (U) from the department of Cesar, Colombia are aberrant in having monocarps and seeds that are somewhat larger than mentioned in the description: monocarps 12–16 by 5–8 mm and seed 13–14 by 6–8 mm!

Juvenile forms of this species tend to have extremely narrow leaves 1.5–2 cm wide, a.o. *Scharf 87* (CAY, LZ, U) and *Fleury 921* (CAY) from French Guiana.

90. *Guatteria longicuspis* R.E.Fr. — Map 22

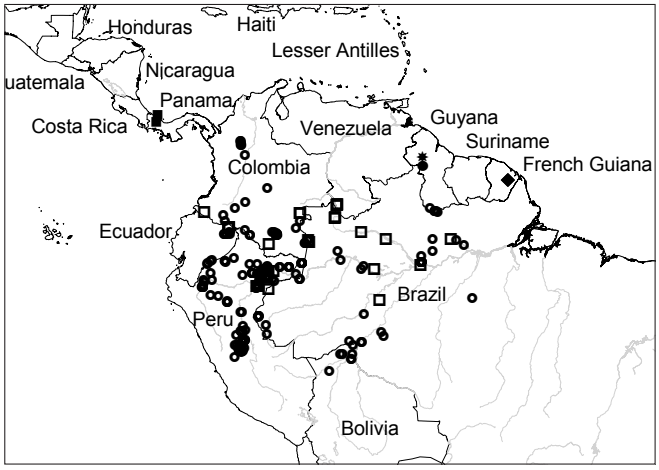
Guatteria longicuspis R.E.Fr. (1900) 18, t. 2, f. 3–5; Maas & Westra (2011) 131, f. 16, pl. 1g. — *Duguetia leptocarpa* Benth. ex R.E.Fr. (1900) 18. — Type: *Spruce s.n.* (holo B; iso BM, K, M, NY, P), Brazil, Amazonas, São Gabriel da Cachoeira, Jan.–Aug. 1852.

Guatteria amazonica R.E.Fr. (1938) 720. — Type: *J.G. Kuhlmann 1564 = RB 24260* (holo S; iso RB 2 sheets), Peru, Loreto, Río Amazonas, Chimbote, 3 Mar. 1924.

Guatteria microcalyx R.E.Fr. (1939) 497, f. 29c, d. — Type: *Krukoff 1033* (holo S; iso BM, G, K, NY, P, S, U), Brazil, Pará, Fordlandia, Boa Vista, Tapajós River region, 6 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 hairs to c. 1 mm long below, base acute to obtuse, or stem-clasping, 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 forming a distinct marginal vein, at a smallest distance of 2–3 mm from the margin, tertiary veins inconspicuous, impressed above, reticulate. *Flowers* solitary, 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 to c. 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, not seen; 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 or 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 papillate. *Monocarps* 25–40, green, maturing dark brown in vivo, brown in sicco, ellipsoid, 17–23 by 4–11{–13} mm, rather densely with appressed hairs, soon glabrous, apex rounded, wall 0.4–0.5 mm thick, stipes 5–10 by c. 1 mm. *Seed* ellipsoid, 13–17 by 7–10 mm, dark brown, longitudinally and transversely grooved to rugulose, raphe not distinct from rest of seed.



Map 22 Distribution of *Guatteria longicuspis* (□), *G. megalophylla* (⭘), *G. pakaraimae* (●), *G. panamensis* (■), *G. pannosa* (◆) and *G. partangensis* (✱).

Distribution — Amazonian Colombia (Amazonas, Caquetá, Vaupés), Venezuela (Amazonas), Ecuador (Napo, Sucumbíos), Peru (Loreto), 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 to October; fruiting: June to February.

Vernacular names — Colombia: Buutruchicu (Muinane name) (*Murillo A. et al. 518*), Ñaatraje dujeku (Muinane name) (*Murillo A. 619*). Peru: Bara (*Rimachi Y. 3593*). Venezuela: Majagua hoja grande (*H.L.Clark 7433*).

Notes — Plants of *G. longicuspis* studied by us are mostly 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 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). In addition to these three species, cauliflory occurs in *G. conspicua* and *G. wachenheimii*, which are quite distinct as mentioned in the notes of those species. Finally *G. scandens*, being a liana, stands on its own in the genus with regard to cauliflory.

The young monocarps of *G. longicuspis* are often pointed (hence Fries's epithet), but the ripe ones are rounded.

The density of the tiny leaf warts (verruculae) is quite variable in this species. Specimens with rather densely verruculose leaves

Fig. 45 *Guatteria macropus* Mart. Flowering branch; details below from left to right: floral receptacle with gynoecium, pistil, ovary in longitudinal section, androecium, stamen abaxial view, stamen adaxial view. – Used as illustration in Martius, Flora Brasiliensis 13, 1 (1841) t. 8. – With kind permission of Botanische Staatssammlung München.

are from Amazonian Ecuador, Peru and one from Colombia (*Balslev 97092*, *Brandbyge 36122*, *Maas 8209*, *Murillo A. 518*, *Vásquez 242*); very densely and more coarsely verruculose leaves are encountered in Amazonian Brazil and Colombia (*Maas 6765*, *6835*, *Prance 17337*, *Schultes 22593*, *24391*, *Zarucchi 1725*).

91. *Guatteria lucens* Standl. — Plate 5d–f; Map 21

Guatteria lucens Standl. (1935) 22; R.E.Fr. (1939) 481, t. 34. — Type: *Cooper 280* (holo F; iso F 2 sheets, G, GH, MO, US), Panama, San Blas, Perma, 27 Apr. 1933.
Guatteria dumetorum R.E.Fr. (1948b) 12, pl. 5. — Type: *Pittier 3915* (holo US 2 sheets; iso F), Panama, Colón, along Río Fato, 10–100 m, 8 July 1911.

Tree 8–38 m tall, 20–60 cm diam; young twigs densely to sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 5–11 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly obovate, 10–21 by 2–6 cm (leaf index 3.5–5), chartaceous, densely or not verruculose, shiny, grey to greyish brown above, brown to greyish brown below, glabrous above, sparsely, sometimes rather densely covered with appressed hairs below, base long-attenuate, basal margins often revolute, apex acuminate (acumen 5–15 mm long), primary vein impressed above, often keeled below, secondary veins distinct, 11–20 on either side of primary vein, raised above, smallest distance between loops and margin 2–4 mm, tertiary veins raised above, reticulate. *Flowers* in 1–3-flowered inflorescences in axils of leaves; pedicels 7–15 mm long, 0.5–1 mm diam, fruiting pedicels 10–35 mm long, c. 1 mm diam, densely, but soon sparsely covered with appressed hairs, articulated at 0.2–0.3 from the base, bracts 5–6, soon falling, rarely third from above foliaceous; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 2–5 by 2–4 mm, reflexed, outer side densely covered with appressed hairs; petals yellow, orange or greenish red in vivo, narrowly ovate to rhombic-ovate, 10–19 by 3–9 mm, outer side densely covered with appressed hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* 40–75, green, red to finally black in vivo, black in sicco, narrowly ellipsoid to ellipsoid, 5–12 by 3–7 mm, rather densely to sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 1 mm long), wall 0.2–0.3 mm thick, stipes 5–20 by 0.5–1 mm. *Seed* ellipsoid, (5–)7–12 by 3–5 mm, dark brown, pitted, raphe raised.

Distribution — Costa Rica, Panama.

Habitat & Ecology — In primary, wet forest. At elevations of 0–900 m. Flowering: January to March, May, July, September, October; fruiting: January, June, July, September, October.

Vernacular name — Panama: Sigui war (Kuna language) (*DeNevers et al. 7578*).

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

Most of the Costa Rican material of this species is characterized by non-verruculose to slightly verruculose leaves, and fits *G. lucens* fairly well. Most collections from Panama (especially those from Colón) and some specimens of the provinces of Puntarenas and Limón in Costa Rica, however, have distinctly verrucose leaves and fall within the concept of *G. dumetorum*. As all other features of these Panamanian collections fit *G. lucens* very well, for this moment – and with hesitation – we have united both species under the oldest name, namely *G. lucens*.

92. *Guatteria macropus* Mart. — Fig. 45; Map 21

Guatteria macropus Mart. (1841) 28, t. 8; R.E.Fr. (1939) 337. — Type: *Martius 712* (holo M; iso B, BM, BR 2 sheets, F, G 2 sheets, HAL, K, L, MO, NY, P, W), Brazil, Bahia, Ilhéus, Fazenda Almada, 9 Jan. 1837.

Tree or shrub 2–13 m tall, 5–15 cm diam; young twigs densely covered with erect, brown hairs, soon glabrous. *Leaves*: petiole 2–10 mm long, 1–2 mm diam; lamina narrowly elliptic to elliptic, 5–18 by 1.5–6.5 cm (leaf index 2.6–7(–10.7)), chartaceous, rather densely verruculose or not verruculose, brown above, pale brown below, glabrous above, densely covered with erect hairs to glabrous below, base obtuse to acute, apex acuminate (acumen 10–15 mm long), primary vein impressed above, secondary veins indistinct, 9–14 on either side of primary vein, raised above, smallest distance between loops and margin 2–5 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 60–120 mm long, c. 1 mm diam, fruiting pedicels to c. 1.5 mm diam, sparsely covered with appressed, brown hairs to glabrous, articulated at 0.1–0.3 from the base, bracts 1–3, soon falling, 5–20 mm long; flower buds broadly ovoid; sepals free, broadly triangular to triangular, 5–10 by 3–9 mm, reflexed, outer side rather densely to sparsely covered with erect hairs; petals pale green or cream in vivo, narrowly elliptic to elliptic, 10–30 by 5–13 mm, outer side densely to sparsely covered with erect, curly, brown hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* 15–25, blackish purple in vivo, black in sicco, ellipsoid, c. 10 by 5 mm, glabrous, apex apiculate (apiculum 0.5 mm long), wall c. 0.3 mm thick, stipes c. 10 by 1 mm. *Seed* ellipsoid, c. 10 by 5 mm, dark brown, pitted, raphe raised.

Distribution — Brazil (Bahia, Espírito Santo, Minas Gerais, Pará).

Habitat & Ecology — In non-inundated, Atlantic rain forest or periodically inundated forest, on clayey soil. At elevations of 10–750 m. Flowering: November to July; fruiting: May to September.

Vernacular names — Brazil: Pindaíba (*Sant'Ana et al. 183*), Pindaíba-preta (*Harley et al. 18351*).

Note — *Guatteria macropus* is characterized by usually very long floral pedicels even up to 120 mm long, causing the flowers to hang from the branches. It resembles *G. australis* by the leaf size. However, *G. macropus* can be distinguished by often longer floral pedicels. *Guatteria candolleana* differs from this species by the cordate leaf base.

93. *Guatteria maguirei* R.E.Fr. — Fig. 36f, g, 46 ; Map 21

Guatteria maguirei R.E.Fr. (1957a) 328; Steyerm. et al. (1995) 446; Murillo A. & Restrepo (2000) 103, f. 30. — Type: *B. Maguire & C.K. Maguire 35657* (holo S; iso F, K, NY, US), Venezuela, Amazonas, Cerro Yutaje, Río Manapiare, Caño Yutaje, 1250 m, 12 Feb. 1953.

Tree or shrub 0.5–6 m tall, diam not recorded; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2–5 mm long, 0.5–1 mm diam; lamina narrowly ovate, 5–9 by 2–3 cm (leaf index 2.4–3.1), coriaceous, not verruculose, shiny above, blackish brown to dark brown above, brown below, glabrous above, sparsely covered with appressed hairs to almost glabrous below, base obtuse, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins distinct, 7–11 on either side of primary vein, raised above, smallest distance between loops and margin 1–2 mm, tertiary venation raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 10–30 mm long, 0.5–1 mm diam, fruiting pedicels to c. 35 mm long, sparsely covered with appressed or with some erect, curly hairs, articulated at 0.2–0.3 from the base, bracts c. 5, soon falling or sometimes present at flowering, broadly elliptic to elliptic, basal bracts c. 1 mm long, upper ones to c. 7 mm long; flower buds depressed ovoid; sepals free, broadly to shallowly ovate-triangular, 2–4 by 3–4 mm, appressed, but finally spreading to apically reflexed, outer side sparsely covered with appressed hairs; petals green, maturing yellow in vivo, ovate to elliptic or narrowly so, 10–22 by

Fig. 46 *Guatteria maguirei* R.E.Fr. Flowering branch (*Huber & Tillett 2967*, U).

3–8 mm, outer side sparsely covered with appressed hairs, but basal part densely so; stamens c. 1 mm long, connective shield papillate. *Monocarps* 10–30, green, maturing black in vivo, black to dark brown in sicco, ellipsoid, 8–9 by 3–6 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum 0.1–0.2 mm long), wall 0.1–0.2 mm thick, stipes 1–2 by 1–2 mm. *Seed* ellipsoid, 5–7 by 3–4 mm, dark brown, pitted to rugulose, raphe impressed.

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

Habitat & Ecology — In shrub islands in savannas and in forest margins adjoining savannas, or in dwarf forest over sandstone with eroded crevices, mostly on white sands. At elevations of 100–1200 m. Flowering: March, May, July, September, November, December; fruiting: March, November, December.

Vernacular name — Venezuela: Majagua (*Velazco 1177a*).

Note — *Guatteria maguirei*, one of the few savanna inhabiting species in the genus, is easily distinguished by its thick and tiny, ovate leaves, combined with relatively long pedicels (up to c. 35 mm long in fruit) and small stipes (up to c. 2 mm long). Like in the probably related *G. atabapensis*, there is a strongly reticulate venation on the upper side of the lamina.

94. *Guatteria maypurensis* Kunth — Fig. 36h, 47; Map 23

Guatteria maypurensis Kunth (1821) 64; R.E.Fr. (1939) 473, f. 24c, d. — Type: *Von Humboldt & Bonpland 902* (holo P; iso B, C, HAL), Venezuela, Amazonas, Maypures.

Annona lanceolata Willd. ex Steud. (1840) 100, nom. nud.

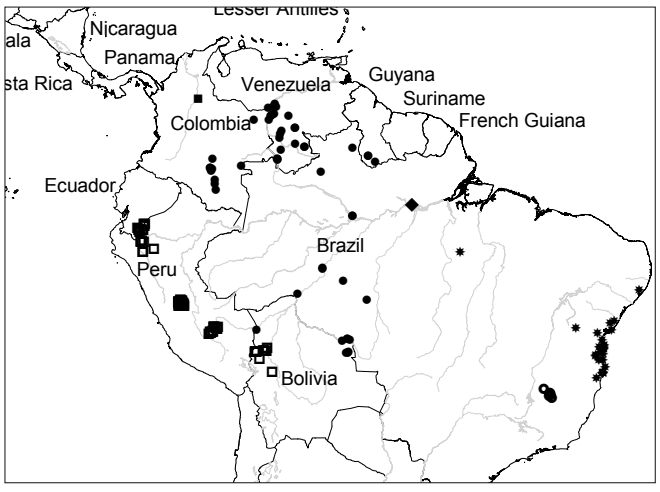
Guatteria maypurensis Kunth var. *attenuata* R.E.Fr. (1939) 474. — Type: *Spruce 3077* (holo K; iso BM, BR, E, F, G, GH, HAL, K, NY, P, W), Venezuela, Amazonas, San Carlos de Río Negro, Sept. 1853.

Guatteria maypurensis Kunth var. *pulchra* R.E.Fr. (1939) 474, t. 33. — Type: *Ducke RB 29048* (holo S; iso MO, RB, SPF), Brazil, Amazonas, Rio Madeira, Humaitá, 29 June 1936.

Guatteria velezii R.E.Fr. (1948b) 8, pl. 3. — Type: *Velez 2488* (holo S; iso US), Venezuela, Bolívar, Parguaza ('Parguasa'), 23 Apr. 1946.

Guatteria calva R.E.Fr. (1948b) 9. — Type: *Ll. Williams 14752* (holo US; iso F, G 2 sheets, NY, RB), Venezuela, Amazonas, Lower Río Casiquiare, Solano, 100 m, 11 Mar. 1942.

Shrub or small tree 1–5(–15) m tall, up to c. 15 cm diam (one specimen up to c. 40 cm!); young twigs glabrous or rarely covered with some scattered, appressed hairs. *Leaves*: petiole 5–15 mm long, 1–1.5 mm diam; lamina often folded lengthwise in herbarium material, narrowly elliptic to elliptic, 5–17 by 2–5.5 cm (leaf index 2–3.6), chartaceous, glabrous, not verruculose, dull, greyish green above, brown below, glabrous above, glabrous or rarely covered with some scattered, appressed hairs below,



Map 23 Distribution of *Guatteria maypurensis* (●), *G. notabilis* (⭘), *G. novogranatensis* (■), *G. oblongifolia* (□), *G. odorata* (◆) and *G. oligocarpa* (✳).

base acute, extreme base long-attenuate, decurrent along petiole, apex mostly bluntly acuminate (acumen 5–10(–20) mm long), primary vein impressed or flat above, sometimes slightly keeled below, secondary veins indistinct, 10–16 on either side of primary vein, raised above, smallest distance between loops and margin 2–4 mm, tertiary veins raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves or rarely on leafless branchlets; pedicels 15–35 mm long, c. 1 mm diam, fruiting pedicels to c. 50 mm long, c. 2 mm diam, glabrous or sometimes covered with some appressed hairs in the basal 0.3, articulated at 0.2–0.5 from the base, bracts 5–6, soon falling, basal bracts broadly elliptic and c. 1 mm, upper ones (narrowly) elliptic or obovate and 6–10 mm long (one specimen seen with more or less foliaceous bract to c. 14 mm long, including short petiole halfway between base and articulation); flower buds depressed ovoid; sepals basally connate, broadly to shallowly ovate-triangular, 3–4 by 3–6 mm, appressed, but the very apex reflexed, outer side sparsely covered with appressed hairs to glabrous, apex more densely hairy; petals green, maturing cream, yellow or brownish in vivo, narrowly oblong-elliptic to obovate, 10–20 by 3–13 mm, outer side densely covered with appressed hairs; stamens 1–1.5 mm long, connective shield papillate to hairy. *Monocarps* 40–70, green, maturing red, black-purple to black in vivo, black to brown in sicco, narrowly oblongoid-ellipsoid, 9–11 by 3–4 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum 0.1–0.2 mm long), wall 0.1–0.2 mm thick, stipes 3–10 by c. 1 mm. *Seed* narrowly oblong-ellipsoid, 8–10 by 3–4 mm, dark brown, shiny, pitted, raphe slightly raised.

Distribution — Colombia (Caquetá, Vichada), Venezuela (Amazonas, Apure), Guyana, Peru (Madre de Dios), Brazil (Amazonas, Goiás, Mato Grosso, Rondônia, Roraima), Bolivia (Beni, Santa Cruz).

Habitat & Ecology — In savannas (in Brazil (Amazonas) dominated by *Antonia ovata*, *Bulbostylis* sp. and *Curatella americana* and in Bolivia (Santa Cruz) dominated by *Cybistax antisyphilitica*, *Brosimum gaudichaudii*, *Curatella americana* and *Simarouba* sp.), sometimes in gallery forest, mostly on sandy soil. At elevations of 0–600 m. Flowering: August to May; fruiting: June to March.

Vernacular names — Venezuela: Majagua (*E. Marín 407*), Majagua verde (*Liesner 6367*).

Field observations — Fruits formerly used for curare (*Schultes et al. 24323* (ECON, GH, MO) from Colombia).

Note — *Guatteria maypurensis* is one of the few species of *Guatteria* that is mostly found in savanna-like vegetations. It is a shrub or small tree, with leaves that are mostly folded lengthwise in dry state; other features are the sepals that are distinctly connate in the basal third and the narrowly oblongoid-ellipsoid monocarps. These features distinguish it from *G. foliosa*, which it more or less resembles.

95. *Guatteria megalocarpa* Maas & Westra, *sp. nov*. — Fig. 48; Map 20

Monocarpiis maximis, ellipsoideis, foliis verruculosis, seminibus rugosis facile recognoscenda. — Typus: *Espinosa & Coba 535* (holo U; iso CR, MO), Ecuador, Pastaza, Cantón Pastaza, Pozo petrolero Namoyacu de UNOCAL, 30 km S of Curaray, 290 m, 13–30 Nov. 1990.

Tree 10 m tall, c. 10 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petioles 15–20 mm long, 1.5–3 mm diam; lamina elliptic, 15–20 by 6–8 cm (leaf index 2.3–2.8), chartaceous to thinly coriaceous, sparsely to rather densely verruculose, more or less shiny, brownish green above, pale brown below, glabrous above, sparsely covered with appressed, whitish hairs mostly on veins below, base obtuse to rounded, the extreme base shortly attenuate into the

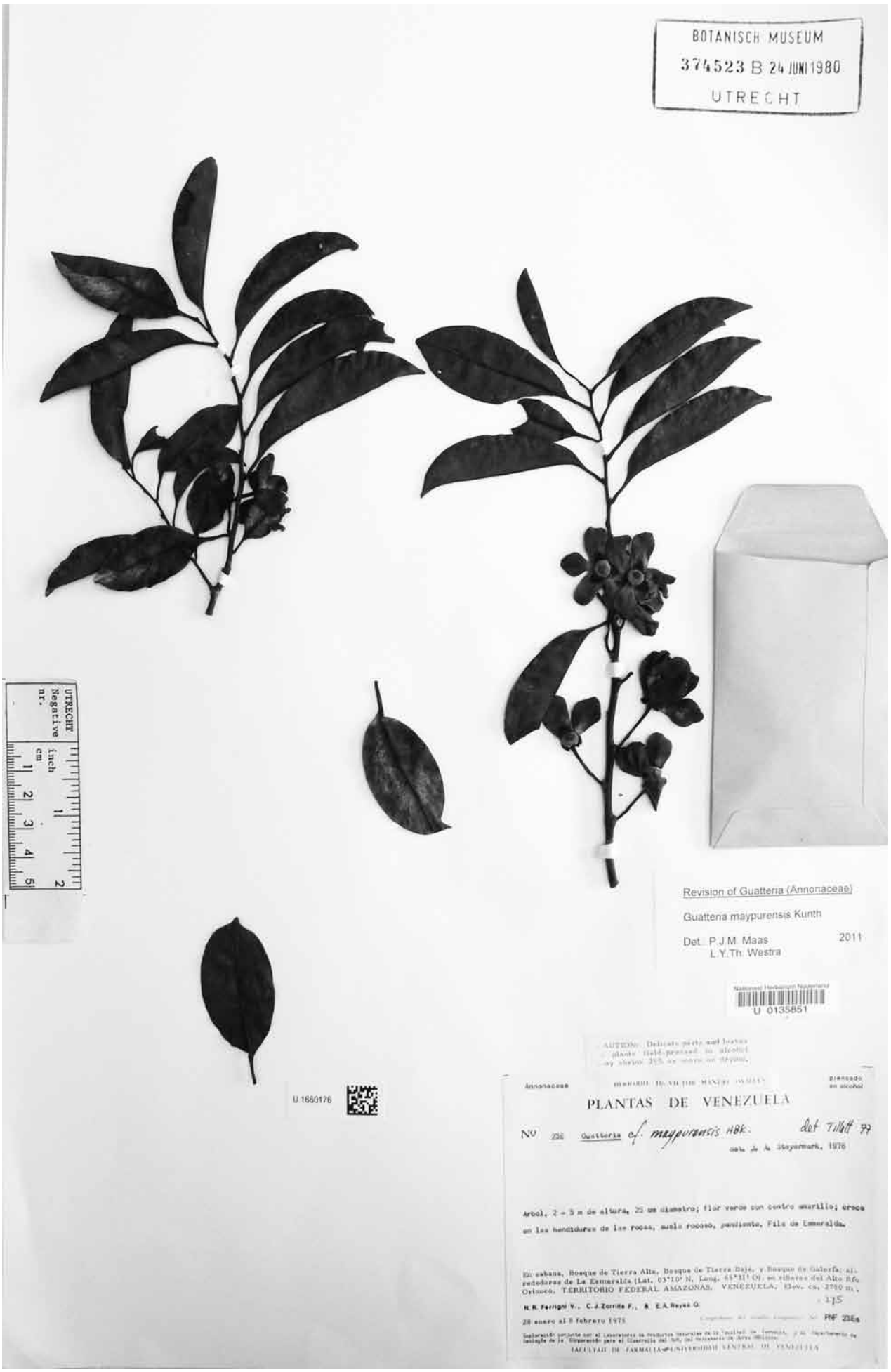


Fig. 47 *Guatteria maypurensis* Kunth. Flowering branch (*Ferrigni V. et al. 23E*, U).

Fig. 48 *Guatteria megalocarpa* Maas & Westra. Fruiting branch (*Espinosa & Coba 535*, holotype U).

petiole, apex acuminate (acumen 10–15 mm long), primary vein flat to slightly impressed above, secondary veins distinct, 13–15 on either side of primary vein, slightly raised above, shortest distance between loops and margin 2–4 mm, tertiary vein raised above, reticulate. *Flowers* only seen in fruiting stage, fruits solitary on leafless branchlets, fruiting pedicels (one complete seen) c. 35 mm long, 2–3 mm diam, glabrous, articulated at c. 0.1 from the base, bracts fallen, no scars visible anymore. *Monocarps* 10–15, dark green in vivo, dark brown in sicco, ellipsoid, 20–23 by 13–15 mm, sparsely covered with appressed hairs to glabrous, apex rounded, wall 1.5–2 mm thick, stipes 12–20 by 2 mm. *Seed* ellipsoid, c. 21 by 13 mm, rugose, raphe impressed.

Distribution — Ecuador (Pastaza).

Habitat & Ecology — In primary, non-inundated forest, on red soil. At an elevation of c. 290 m. Flowering: unknown; fruiting: November.

Vernacular name — Ecuador: Heñetangueme (Huaorani name) (*S. Espinoza & Coba 535*).

Note — The single collection known to us so far was listed as 'sp. indet.' in the revision of sect. *Mecocarpus* (Maas & Westra 2011). Despite its incompleteness we see sufficient reason for formally describing it as a new species now. *Guatteria megalocarpa* is quite well characterized by the conspicuously large and ellipsoid monocarps, not matched in any other species of this section. It seems to come closest (also when following the key in the paper cited) to *G. blepharophylla*, but differs from that by the much longer pedicels, and by the monocarps, which, although of comparable length, are relatively broader (described here as 'ellipsoid' vs 'narrowly ellipsoid' in *G. blepharophylla*). The seeds in *G. megalocarpa* are evenly rugose, as contrasted to the seeds in *G. blepharophylla*, which tend to be longitudinally and/or transversely grooved.

96. *Guatteria megalophylla* Diels — Fig. 49, 50; Plate 5g, h; Map 22

Guatteria megalophylla Diels (1905) 127; R.E.Fr. (1939) 487, f. 26c; Maas et al. (1993) 84; Murillo A. & Restrepo (2000) 106, f. 31; Erkens et al. (2008) 502, f. 14. — Type: *Ule 5630* (holo B; iso BM, G, L 2 sheets, MG, U), Brazil, Acre, Rio Jurua-Mirim, July 1901.

Guatteria melosma Diels (1927) 170; R.E.Fr. (1939) 485, f. 26a, b. — Type: *Tessmann 5039* (holo B; iso F, G, NY), Peru, Loreto, Iquitos, 100 m, Feb. 1925.

Guatteria megalophylla Diels var. *deminuta* R.E.Fr. (1939) 488, f. 26d, e. — Type: *Krukoff 6388* (holo S; iso BM, BR, F, G, K, MO, NY, U, US), Brazil, Amazonas, Mun. Humaitá, Basin of Rio Madeira, Três Casas, 14 Sept. 1934.

Tree 3–15 m tall, to c. 25 cm diam; young twigs densely to rather densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 15–50 mm long, 3–10 mm diam, often winged; lamina narrowly elliptic, 20–75 by 5–30 cm (leaf index 2.5–5.6), chartaceous, not verruculose, slightly shiny, greyish green to brown above and below, glabrous above, rather densely to sparsely covered with appressed hairs to glabrous below, base acute to obtuse, often distinctly attenuate, apex acuminate (acumen 15–20 mm long), primary vein impressed above, secondary veins distinct, 15–35 on either side of primary vein, strongly impressed above, forming a distinct marginal vein, at a smallest distance of 2–4 mm from the margin, tertiary veins inconspicuous, slightly raised above, reticulate to percurrent. *Flowers* in 1(–2)-flowered inflorescences on leafless branchlets or less often in axils of leaves; pedicels 5–10 mm long, 2–3 mm diam, fruiting pedicels 15–20 mm long, 3–6 mm diam, densely covered with appressed hairs, becoming glabrous, articulated at 0.3–0.4 from the base, bracts 6–7, soon falling, only basal bract rarely seen, very broadly ovate, c. 1 mm long; flower buds ovoid to broadly ovoid, slightly pointed; sepals free, broadly ovate-triangular, 6–12 by 6–12 mm, appressed, outer side densely covered with appressed hairs; petals greenish yellow, yellow, orange or red in vivo, ovate, elliptic to rhombic, 15–27 by 10–15 mm, outer side densely covered with appressed hairs; stamens c. 2 mm long, connective shield papillate, sometimes umbonate. *Monocarps* 10–25, green, maturing purplish black to black in vivo, black to brown in sicco, ellipsoid, 15–40 by 8–18 mm, rather densely to sparsely covered with appressed hairs, soon glabrous, apex rounded to apiculate (apiculum < 0.5 mm long), wall c. 1 mm thick, stipes 1–7 by 1–4 mm. *Seed* ellipsoid, 12–25 by 7–14 mm, dark, shiny brown, longitudinally and transversely grooved to rugose, raphe not distinct from rest of seed.

Distribution — Colombia (Amazonas, Antioquia, Caquetá, Putumayo, Vaupés), S Guyana, Amazonian Ecuador (Morona-Santiago, Napo, Sucumbíos), Peru (Amazonas, Huánuco, Junín, Loreto, Pasco, San Martín, Ucayali), Brazil (Acre, Amapá, Amazonas, Pará, Rondônia, Roraima), Bolivia (Beni, La Paz, Pando).

Habitat & Ecology — In non-inundated or rarely periodically inundated forest, on sandy to clayey soil. At elevations of 0–1500 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Bolivia: Arbol de agua (*Solomon 6401*). Brazil: Envira (*Krukoff 6388*). Colombia: Carguero (*Murillo A. 532*), Cherimoya (*Schultes 3645*), Garapato (*Vera-Sánchez et al. 229*), Garapato negro (*Vera-Sánchez et al. 445*), Iyuku dujeku (Muinane name) (*Murillo A. 532*), Majagua (*Vera-Sánchez et al. 216*). Ecuador: Cara caspi (*Korning & Thomsen 58629*), Yais (Shuar name) (*Neill et al. 16391*). Peru: Anona (*Rimachi Y. 2443*), Anonilla (*J.C. Ruiz 1313*), Auca hicoja (*Schunke V. 5889*), Bara (*McDaniel 17468*, *Rimachi Y. 907*), Bara caspi (*McDaniel 20201*, *Rimachi Y. 6110*, *8523*, *11765*), Carahuasca (*Díaz M. 42*, *Pariona & Ruiz 1002*, *Reynel R. 47*, *407*, *629*, *J.C. Ruiz 1313*, *Schunke V. 4990*, *Simpson & Schunke V. 756*, *Vásquez et al. 6614*, *7508*, *7992*, *9503*, *10384*), Chiuanim (*Kayap 649*), Chiwanim (*Ancuash 28*, *364*, *418*), Espintana (*Rimachi Y. 3763*, *9286*), Espintana de hoja ancha (*Maas et al. 4531*, *Young & Grández 1042*), Icoja blanca (*Begazo 122*), Sacha aguaja (*Daly 5702*), Tintuk (*Kayap 646*), Tortuga caspi (*Rimachi Y. 1064*, *1156*, *1300*), Vara (*Vásquez et al. 7343*, *7344*, *7347*), Washi yais (Huambisa name) (*Tunqui 907*), Yais (*Kajekai 909*), Yana baru (*Rimachi Y. 3486*).

Note — *Guatteria megalophylla* is a species very widely spread all over Amazonian America (Colombia, Ecuador, Peru, Brazil and in Guyana), mostly at low elevations up to 600 m. It is easily recognizable by having very large leaves (of up to 75 by 20 cm!) with a very distinct and impressed marginal vein, rather long petioles, shortly pedicellate flowers (mostly produced from leafless branchlets) and shortly stipitate monocarps.

97. *Guatteria meliodora* R.E.Fr. — Map 20

Guatteria meliodora R.E.Fr. (1939) 500; Spichiger et al. (1989) 124, f. 58; Maas et al. (2007) 640; Maas & Westra (2011) 135, f. 17. — Type: *Krukoff 5050* (holo S; iso BM, F, G, K, M, MO, NY, U, US), Brazil, Amazonas, Basin of Rio Juruá, near mouth of Rio Emvira, 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 shortly acuminate (acumen to c. 5 mm long),

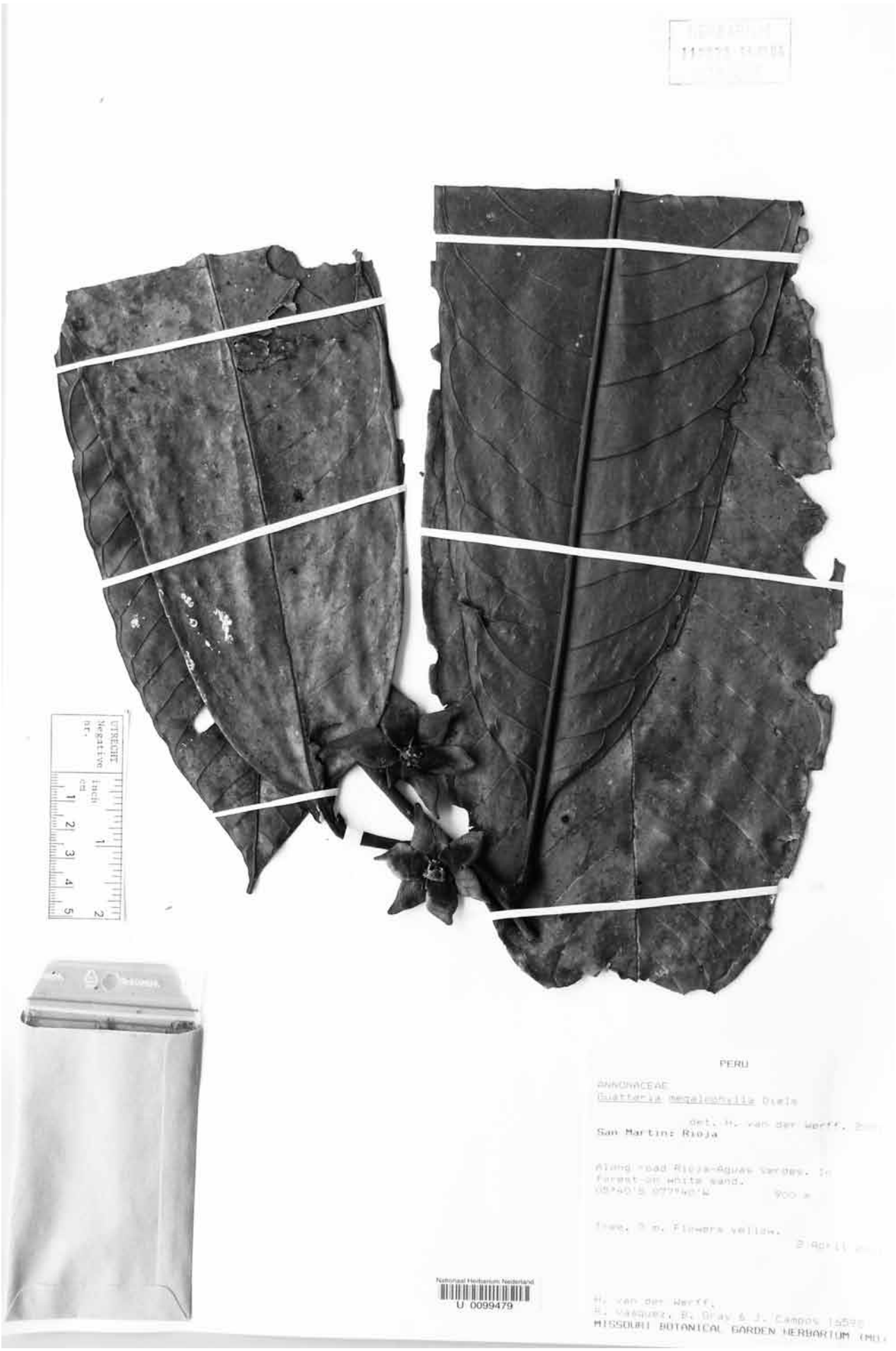


Fig. 49 *Guatteria megalophylla* Diels. Flowering branch (*Van der Werff et al. 16592*, U).

Fig. 50 *Guatteria megalophylla* Diels. Fruiting branch (*Solomon 6401*, U).

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, tertiary veins slightly raised above, percurrent to reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; pedicels 10–20 mm long, c. 2 mm diam, fruiting pedicels to c. 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 uppermost 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, soon 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, Amazonian Peru (Loreto), Brazil (Acre, Amazonas).

Habitat & Ecology — In non-inundated forest, sometimes campinarana forest or savanna 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 et al. 1772*).

Notes — *Guatteria meliodora* is distinct 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. It resembles *G. dura*, both species falling within sect. *Mecocarpus*. 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, might belong here, but this sterile collection is aberrant in having a strongly attenuate leaf base.

98. *Guatteria microcarpa* Ruiz & Pav. ex G.Don — Map 20

Guatteria microcarpa Ruiz & Pav. ex G.Don (1831) 100; R.E.Fr. (1939) 337, f. 7c, d; Erkens et al. (2008) 503, f. 15. — Type: *Ruiz L. s.n.* (holo B; iso BR, G, HAL), Ecuador, Guayas, Guayaquil ('Huayaquil'), anno 1800.
Guatteria sodiroi Diels (1907) 42; R.E.Fr. (1939) 338, f. 7a, b, syn. nov. — Type: *Sodiro 18* (holo B 2 sheets), Ecuador, Chimborazo, Pallatanga, 400–500 m, Sept. 1891.
Guatteria sp. 15 Chatrou et al. (1997) 112.

Tree or shrub 2–8(–14) m tall, to c. 10 cm diam; young twigs densely to sparsely covered with erect, brown hairs, eventually glabrous. *Leaves*: petiole 3–6 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly obovate, 10–25 by (3–)5–10 cm (leaf index 2–3.6), chartaceous, not verruculose, somewhat shiny, dark green, greyish green or greyish brown above, pale to dark brown below, sparsely covered with appressed and erect hairs, particularly along primary and secondary veins above, rather densely to sparsely covered with erect, brown hairs below, base obtuse, sometimes acute, apex acuminate (acumen 5–20 mm long), primary vein impressed above, secondary veins distinct, 10–15 on either side of primary vein, impressed to sometimes flat above, smallest distance between loops and margin 2–5 mm, tertiary veins slightly raised above, reticulate. *Flowers* in 1(–3)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 20–50 mm long, 0.5–2 mm diam, fruiting pedicels to c. 65 mm long, c. 3 mm diam, densely covered with erect hairs, becoming glabrous in age or not, articulated at 0.2–0.3 from the base, bracts c. 5, soon falling, uppermost bract elliptic, c. 4 mm long, basal bract broadly ovate-elliptic, c. 1 mm; flower buds broadly ovoid; sepals free or basally connate, broadly ovate-triangular, 5–7{–9} by 5–7{–9} mm, appressed to spreading, outer side densely covered with appressed hairs; petals green, maturing cream in vivo, elliptic-obovate to obovate-oblong, 12–23 by 8–15 mm, outer side densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate to hairy. *Monocarps* 30–50, dark green, maturing black to purple-black in vivo, black in sicco, ellipsoid, 8–10 by 5–6 mm, glabrous, except for some scattered, appressed hairs, particularly at the apex, apex apiculate (apiculum < 0.5 mm long), wall 0.2–0.3 mm thick, stipes red to purple, 12–25 by c. 1 mm. *Seed* ellipsoid, 8–9 by 5–6 mm, pale to dark brown, pitted, raphe slightly raised.

Distribution — Western Ecuador (Cañar, Cotopaxi, Esmeraldas, Guayas, Los Ríos, Manabí, Napo?), adjacent Colombia (Nariño).

Habitat & Ecology — In non-inundated, lowland or premontane, primary or secondary forest ('bosque húmedo tropical' or 'bosque muy húmedo premontano'). At elevations of 0–1000 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular name — Ecuador: Punta de lanza.

Uses — Ecuador: Sap of the leaves is used to cure wounds ('El zumo de las hojas se usa para curar heridas') (*Alvarez et al. 89*). Fishing rods are made of the stems ('El tallo sirve para hacer lanzas para pescar') (*Cornejo & Bonifaz 4869*).

Notes — *Guatteria microcarpa* was placed by Fries in sect. *Trichoclonia* because of the rather conspicuous brown hairs on the young twigs. Apart from the indument, it can be recognized by leaves with impressed secondary veins on the upper side, and by relatively long and slender pedicels.

We have added *G. sodiroi* in the synonymy as almost all features fit very well within the concept of *G. microcarpa*, the only minor difference being an acute leaf base instead of obtuse, as is mostly the case in *G. microcarpa*. However, in *G. microcarpa* an acute leaf base occurs occasionally, too.

One collection from Napo, Ecuador, *Bensman 210* (MO) may belong here.

99. *Guatteria minutiflora* Scharf & Maas — Map 20

Guatteria minutiflora Scharf & Maas in Scharf et al. (2006a) 124, f. 4. — Type: *Henkel et al. 1156* (holo U; iso BRG, CAY, US), Guyana, Potaro-Siparuni Region, Pakaraima Mts, Upper Ireng River, 2 km E of Cipo settlement on N end of adjacent ridge, 750 m, 3 Feb. 1993.

Tree 4–15 m tall, diam not recorded; young twigs sparsely to densely covered with erect, dark brown hairs, soon glabrous. *Leaves*: petiole 3–7 mm long, 1–1.5 mm diam; lamina narrowly elliptic to ovate, 5–11 by 2–4 cm (leaf index 2.9–3.6), chartaceous, not verruculose, dull, mostly greyish black on both sides, glabrous above, except for some erect, brownish hairs along primary vein, sparsely covered with erect hairs below, base acute, slightly attenuate, apex acuminate (acumen 5–15 mm long), primary vein flat to slightly impressed above, secondary veins indistinct, 7–10 on either side of primary vein, raised above, smallest distance between loops and margin 1–3 mm, tertiary veins raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; pedicels 7–15 mm long, 0.5–1 mm diam, fruiting pedicels 10–20 mm long, c. 1 mm diam, rather densely covered with erect hairs, articulated at 0.3–0.5 from the base, bracts 5–6, soon falling, only basal ones seen, triangular-ovate, to c. 1 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–4 by 3–4 mm, apically reflexed, outer side densely covered with appressed, reddish brown, long hairs; petals green with

purple base in vivo, oblong-ovate, 5–15 by 3–7 mm, outer side densely covered with appressed hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* 10–40, green in vivo, black to dark reddish brown in sicco, ellipsoid, 7–12 by 4–5 mm, glabrous, apex apiculate (apiculum < 1 mm long), wall 0.1–0.2 mm thick, stipes 5–15 by c. 0.5 mm. *Seed* ellipsoid to ovoid, 8–10 by 4–5 mm, brown, smooth, pitted or rugulose, raphe not distinct from rest of seed.

Distribution — Western Guyana and Central Suriname.

Habitat & Ecology — In forest on mountain tops or on slopes, in association with *Euterpe*, *Inga*, *Licania*, *Schefflera*, *Socratea* and *Weinmannia*, on sandstone with peat and sandy clay or lateritic soil. At elevations of 750–1500 m. Flowering: January to March, June; fruiting: January to March, June.

Vernacular names — Not recorded.

Notes — *Guatteria minutiflora* is quite characteristic by its small, often more or less black drying leaves, an indument of erect, brown hairs on the leafy twigs and lower leaf side, and by its small petals in comparison to *Guatteria* species in general. It somewhat resembles *G. liesneri* notably in its dark drying leaves, but it lacks the strongly raised tertiary veins of the latter.

100. *Guatteria modesta* Diels — Map 24

Guatteria modesta Diels (1924b) 139; R.E.Fr. (1939) 430; Maas & Westra (2010) 269, f. 7. — Type: *Tessmann 3476* (holo B 2 sheets; iso G 2 sheets, NY, S, US), Peru, Ucayali, Yarina Cocha, 150 m, 27 Dec. 1923.

Guatteria chlorantha Diels (1924b) 139; R.E.Fr. (1939) 422, f. 14d. — Type: *Tessmann 3423* (holo B; iso G, NY, S, US), Peru, Ucayali, Yarina Cocha, 150 m, 7 Dec. 1923.

Guatteria tessmannii R.E.Fr. (1938) 713; (1939) 420, t. 29, syn. nov. — Type: *Tessmann 4651* (holo B 2 sheets; iso G, NY, S), Peru, Amazonas, Upper Río Marañon, mouth of Río Santiago, 160 m, 26 Nov. 1924.

Guatteria geminiflora R.E.Fr. var. *geminiflora* (1939) 421. — Type: *Tessmann 4314* (holo B 2 sheets; iso NY), Peru, Amazonas, mouth of Río Santiago, 160 m, 16 Oct. 1924.

Guatteria geminiflora R.E.Fr. var. *ochrantha* R.E.Fr. (1939) 422, syn. nov. — Type: *Mutis 4486* (holo US; iso S, fragment), Colombia, without location.

Guatteria puncticulata R.E.Fr. (1939) 511, f. 33b, c. — Type: *Krukoff 8225* (holo S; iso BM, BR, F, G, K, MO, NY, U, US), Brazil, Amazonas, Mun. São Paulo de Olivença, near Palmares, 11 Sept.–26 Oct. 1936.

Guatteria glaberrima R.E.Fr. (1947) 3. — Type: *Lugo 237* (holo S; iso G, S, US), Ecuador, Pastaza, Mera, 25 Apr. 1940.

Guatteria sp. 16 Chatrou et al. (1997) 112.

Tree 8–55 m tall, up to c. 1 m diam, sometimes with buttresses up to c. 80 cm high; young twigs often black, sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 5–10 mm long, c. 1 mm diam; lamina narrowly obovate to narrowly elliptic, 7–19 by 2–6 cm (leaf index 3–5.3), chartaceous to coriaceous, not to densely verrucose, blackish brown, brown to greyish brown above, brown to dark brown below, glabrous above, sparsely or rarely rather densely covered with appressed hairs to glabrous below, the primary vein sometimes covered with long hairs, margins glabrous or sometimes covered with long hairs, base long-attenuate and margins strongly revolute, apex acuminate (acumen 5–10 mm long), primary vein impressed above, raised and often keeled below, secondary veins indistinct, 10–18 on either side of primary vein, flat to slightly raised above, smallest distance between loops and margin 2–3 mm, tertiary veins inconspicuous, flat to slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–25 mm long, 1–2 mm diam, fruiting pedicels to c. 3 mm diam, sparsely or rarely rather densely covered with appressed hairs to glabrous, articulated at c. 0.2 from the base, bracts 6–7, soon falling, uppermost bracts elliptic-obovate to elliptic, 5–9 mm long, basal bracts broadly ovate, to c. 1 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular to ovate-triangular, 3–9 by 3–6 mm, appressed, finally reflexed, outer side densely covered with appressed hairs; petals green, maturing cream or yellow in vivo, narrowly oblong-elliptic to oblong-elliptic, 15–30 by 4–13 mm, outer side densely covered with appressed hairs; stamens 1–2 mm long, connective shield papillate to glabrous. *Monocarps* 10–50, green, maturing black in vivo, black in sicco, ellipsoid, 9–15 by 6–10 mm, surface somewhat wrinkled when ripe, glabrous, apex rounded, wall 0.5–1 mm thick, stipes 8–20 by c. 1 mm. *Seed* ellipsoid, 8–11 by 5–7 mm, dark brown, smooth to slightly pitted, raphe not distinct from rest of seed.

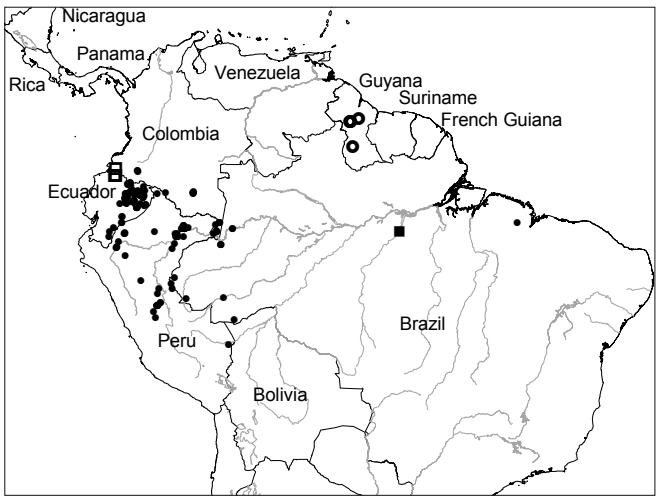
Distribution — Amazonian Colombia (Amazonas, Caquetá), Ecuador (Morona-Santiago, Napo, Pastaza, Sucumbios), Peru (Amazonas, Huánuco, Loreto, Madre de Dios, Pasco, Ucayali), Brazil (Acre, Amazonas, Maranhão).

Habitat & Ecology — In non-inundated, lowland rain forest or submontane forest, often on red soil. At elevations of 100–1250 m. Flowering: throughout the year; fruiting: July to January.

Vernacular names — Brazil: Chaporoasca (*Daly et al. 7729*). Colombia: Espintana (*Rudas et al. 3416*, *3427*), Spintana (*Rudas et al. 3516*). Ecuador: Caracaspi (*Freire & Inmunda 3210*, *H. Vargas et al. 569*), Fandicho (Cofán) (*Cerón 21161*), Gañitahuemo (Huaorani name) (*M. Aulestia & Gonti 1752*), Homñetahue (Huaorani name) (*Espinoza & Coba 617*), Minudawa (Huaorani name) (*King et al. 975*), Oñetahue (Huaorani name) (*M. Aulestia et al. 1445*), Oñitahue (Huaorani name) (*M. Aulestia et al. 3041*), Runa caspi (*Freire at al. 3392*), Uñetahue (Huaorani name) (*Gudiño et al. 824*), Uñitahue (Huaorani name) (*M. Aulestia & Bainca 3551*). Peru: Carahuasca (*Aróstegui V. 127*, *Aspajo V. 15*, *Hartshorn 1665*), Carahuasca negra (*Reyna R. 62*), Espintana (*Tessmann 3476*), Espintana hoja ancha (*Soria S. 11*), Wampuyais (Shuar name) (*Kayap 850*), Yais (Huambisa name) (*C. Díaz et al. 7390*), Yam yais (Huambisa name) (*Tunqui 194*), Yeis (Huambisa name) (*Huashikat 2161*), Yumi yeis (Huambisa name) (*Huashikat 879*).

Notes — Contradictory to what the name might suggest, *G. modesta* contains some of the tallest trees within the genus, reaching a height of up to 55 m and a diameter up to 1 m! By contrast, most *Guatterias* are small to medium-sized trees, with only relatively few species having been reported as tall trees with a trunk up to 50 cm diam. *Guatteria modesta* can easily be recognized by its long-attenuate, often narrowly obovate leaves which have a quite dark colour when dry.

Various specimens from Ecuador (Pastaza, Sucumbios), Peru (Amazonas, Loreto, Ucayali) and Brazil (Acre, Amazonas) fall within Fries's concept of *G. puncticulata*. They differ from typical *G. modesta* by densely verruculose leaves with the margins and the primary vein (on the lower side) often covered with



Map 24 Distribution of *Guatteria modesta* (●), *G. monticola* (⭘), *G. myriocarpa* (■) and *G. narinensis* (□).

long hairs. Nevertheless, these should be regarded as more extreme forms of *G. modesta* as several intermediate forms have been found, too.

101. *Guatteria monticola* R.E.Fr. — Map 24

Guatteria monticola R.E.Fr. (1952a) 395. — Type: *Forest Department British Guiana 5882 = Wilson-Browne 473* (holo NY 2 sheets; iso FDG, K, S), Guyana, Kanuku Mts, Wabuwak, '2000 ft.', Nov. 1948.

Tree 5–30 m tall, 10–25 cm diam; young twigs densely covered with appressed to erect, brown hairs to c. 2 mm long, soon glabrous. *Leaves*: petiole 4–10 mm long, 1–2 mm diam; lamina narrowly elliptic, 11–18 by 4–7 cm (leaf index 2.6–3.6), chartaceous, not verruculose, dull, greyish pale brown to dark brown above, dark brown below, glabrous above, but primary vein densely covered with erect, brown hairs, densely covered with appressed, brown hairs to c. 1 mm long below, base acute, apex acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 10–13 on either side of primary vein, flat to slightly impressed above, smallest distance between loops and margin 1–2 mm, tertiary veins flat above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves, occasionally also on leafless branchlets; pedicels 10–25 mm long, c. 1 mm diam, fruiting pedicels to c. 3 mm diam, densely covered with appressed to erect, brown hairs, articulated at 0.2–0.5 from the base, bracts 5–6, soon falling, broadly ovate, the 2 uppermost ones c. 3 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–7 by 4–6 mm, appressed, outer side densely covered with appressed, brown hairs; petals green or yellowish green in vivo, ovate to elliptic to narrowly so, 10–26 by 6–10 mm, outer side densely covered with appressed, brown hairs; stamens c. 1 mm long, connective shield papillate, umbonate or not. *Monocarps* 30–50, black in vivo, black to dark brown in sicco, ellipsoid, 5–7 by 3–4 mm, sparsely covered with appressed hairs, soon glabrous, apex bluntly apiculate (apiculum 0.1–0.5 mm long), wall 0.1–0.2 mm thick, stipes 5–15 by 0.5–1 mm. *Seed* ellipsoid, 6–7 by 4 mm, shiny brown, pitted to slightly transversely grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Venezuela (Amazonas, Bolívar), Guyana, Suriname.

Habitat & Ecology — In non-inundated forest or in savannas (in Guyana) on rocky outcrops or on sandy soil. At elevations of 0–700 m. Flowering: May, October, November; fruiting: March, October.

Vernacular names — Not recorded.

Note — *Guatteria monticola* looks very similar to *G. procera*, but is distinct in a number of features. For further explanation, see under the latter.

102. *Guatteria myriocarpa* R.E.Fr. — Map 24

Guatteria myriocarpa R.E.Fr. (1939) 458, t. 32. — Type: *Dahlgren & Sella 119* (holo B; iso F), Brazil, Pará, Rio Tapajós, Boa Vista, May–June 1929.

Tree c. 10 m tall, c. 25 cm diam; young twigs densely covered with appressed hairs to c. 0.5 mm long, eventually glabrous. *Leaves*: petiole 3–5 mm long, 1–2 mm diam; lamina narrowly elliptic, 8–16 by 2–4.5 cm (leaf index 3.2–5.5), chartaceous, not verruculose, dull, blackish brown to greyish brown above, brown below, sparsely covered with appressed hairs above, the primary vein rather densely covered with erect, brown hairs above, rather densely covered with appressed hairs below, base acute to obtuse, apex acuminate (acumen 10–20 mm long), primary vein impressed above, secondary veins distinct, 13–15 on either side of primary vein, slightly raised above, smallest distance between loops and margin 2–4 mm, tertiary veins slightly raised above, reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; pedicels 12–15 mm long, c. 1 mm diam, fruiting pedicels not seen, rather densely covered with appressed hairs, articulated at c. 0.5 from the base, bracts c. 5, soon falling, not seen; flower buds not seen; sepals free, broadly ovate-triangular to ovate-triangular, 5–6 by 4 mm, reflexed, outer side densely covered with appressed hairs; petals colour not recorded, obovate to elliptic, 13–18 by 6–10 mm, outer side rather densely covered with appressed hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* c. 50, colour in vivo not recorded, black in sicco, ellipsoid, 7–9 by 3–4 mm, sparsely covered with appressed hairs, apex apiculate (apiculum < 0.5 mm long), wall c. 0.1 mm thick, stipes 15–25 by 0.5–1 mm. *Seed* ellipsoid, c. 7 by 4 mm, brown, slightly pitted, raphe not distinct from rest of seed.

Distribution — Amazonian Brazil (Amazonas, Pará).

Habitat & Ecology — In non-inundated forest ('firm land'). At an elevation of c. 40 m. Flowering: May, June; fruiting: September.

Vernacular name — Brazil: Juruá-cacauo (*Capucho 433*).

Notes — *Guatteria myriocarpa* belongs to Fries's sect. *Brachystemon*, characterized by young twigs densely covered with appressed and erect hairs and by small flowers and fruit for the genus. Of the 6 species of this section 5 occur in SE Brazil, the most common one being *G. sellowiana*.

Guatteria myriocarpa much resembles *G. hirsuta*, but differs by the indument on young twigs, which consists of mainly appressed hairs of up to c. 0.5 mm long, vs erect hairs 1.5–2 mm long in *G. hirsuta*.

103. *Guatteria narinensis* Maas & Westra, *sp. nov.* — Fig. 51; Map 24

Species foliis fuscobrunneis (in siccitate) basi acutis vel longe attenuatis dense verruculosis interdum plusminusve in lineis coalitis, pedicellis gracilibus pro ratione longis notabilis. — Typus: *Maas et al. 6521* (holo U 2 sheets; iso COL, K, NY), Colombia, Nariño, 10 km before La Guayacana, 450 m, 10 June 1986.

Guatteria sp. 11 Chatrou et al. (1997) 111.

Tree 6–25 m tall, to c. 50 cm diam; young twigs densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 1–3 mm long, 1–2 mm diam; lamina narrowly elliptic, 10–19 by 2–4 cm (leaf index 4–6), chartaceous, densely verruculose, the warts often arranged in lines, dull, dark brown above, brown below, glabrous above, but primary vein densely to sparsely covered with erect hairs above, sparsely covered with appressed hairs to subglabrous below, but primary vein densely covered with appressed hairs, base acute to long-attenuate, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins indistinct, 15–20 on either side of primary vein, flat to slightly raised above, smallest distance between loops and margin 1–2 mm, tertiary veins flat above, reticulate. *Flowers* solitary in axils of leaves; pedicels 25–45 mm long, 1–2 mm diam, fruiting pedicels c. 45 mm long, c. 2 mm diam, rather densely covered with appressed hairs, articulated at 0.2–0.4 from the base, bracts 4–6, soon falling, uppermost bract (one seen) obovate, c. 4 mm long, a persisting foliaceous bract c. 20 mm long, seen on one pedicel, inserted just below the uppermost bract; flower buds depressed ovoid to ovoid; sepals free, broadly ovate-triangular, 5–6{–9} by 6–7{–10} mm, appressed, outer side densely to rather densely covered with appressed hairs; petals yellowish green or yellow in vivo, ovate, 12–14{–25} by 8–11{–18} mm, outer side densely (near the base) to rather densely covered with appressed hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* c. 40, colour in vivo not recorded, brownish in sicco, ellipsoid, {7–9} by {4–5} mm, sparsely covered with appressed hairs, apex

Fig. 51 *Guatteria narinensis* Maas & Westra. Flowering branch (*Maas et al. 6521*, holotype U).

apiculate (apiculum < 0.5 mm long), wall {0.4–0.6} mm thick, stipes 5–6 by c. 1 mm. *Seed* ellipsoid, c. 7 by 4 mm, black, pitted, raphe not distinct from rest of seed.

Distribution — Western Colombia (Nariño), Ecuador (Carchi, Esmeraldas).

Habitat & Ecology — In non-inundated, primary or secondary forest, on clayey soil with boulders. At elevations of 250–450 m. Flowering: March, June; fruiting: March, June.

Vernacular names — Ecuador: Guarea negra (*C. & M. Aulestia 1251*), Palay (*Játiva 323*).

Other specimens examined. Ecuador, **Esmeraldas**, San Lorenzo, Reserva Etnica Awá, Parroquia Alto Tambo, Centro de la Unión, Cañón del Río Mira, 250 m, *C. & M. Aulestia 1251* (U); Tobar Donoso, 225 m, *Játiva 323* (NY); Tobar Donoso, junction of Río San Juan and Rio Cabumbi, 150 m, *Játiva & Epling 1126* (MO, NY); border area between provinces Carchi and Esmeraldas, 30 km past Lita, on road from Lita to Alto Tambo, 450 m, *Van der Werff et al. 12128* (MO, U).

Note — *Guatteria narinensis* is very easily recognizable by narrow, densely verruculose leaves, which become brown to dark brown upon drying, and by relatively long pedicels up to c. 45 mm long.

104. *Guatteria notabilis* Mello-Silva & Pirani — Map 23

Guatteria notabilis Mello-Silva & Pirani (1988) 44, f. 1–23. — Type: *Mello-Silva et al. CFCR 8062* (holo SPF; iso BHCB, CEPEC, F, K, MO, NY, OWU, RB, SP, SPF 2 sheets, U), Brazil, Minas Gerais, Joaquim Felício, Serra do Cabral, road to Várzea da Palma, 1000 m, 31 Aug. 1985.

Tree 4–9 m tall, 5–30 cm diam; young twigs densely covered with erect, long-persisting, brown hairs, finally glabrous. *Leaves*: petiole 2–5 mm long, 1–3 mm diam; lamina narrowly oblong-elliptic, rarely elliptic, 10–20 by 3.5–6 cm (leaf index 2.5–3.4), coriaceous, densely verruculose, dull, greyish green to brown above, dark brown below, sparsely covered with erect hairs above, densely covered with erect, brown hairs below, base obtuse to rounded, extreme base slightly attenuate, basal margins slightly revolute, apex acute, obtuse, or shortly acuminate (acumen 2–5 mm long), the very apex revolute and mucronate (mucro 1–2 mm long), primary vein raised to flat above, secondary veins indistinct, 12–18 on either side of primary vein, flat above, smallest distance between loops and margin 2–4 mm, tertiary veins inconspicuous, flat above, reticulate. *Flowers* in 1–3-flowered, terminal inflorescences; pedicels 10–20 mm long, c. 2 mm diam, fruiting pedicels to c. 25 mm long, c. 3 mm diam, densely covered with erect hairs, articulated at c. 0.2 from the base, bracts 2, soon falling, sometimes foliaceous, elliptic to obovate-elliptic, 10–22 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 10–15 by 7–11 mm, appressed (but according to *Pirani et al. CFCR 11147*: reflexed and revolute), outer side densely covered with erect hairs; petals greenish, cream or reddish green in vivo, elliptic to broadly elliptic, 10–18 by 8–13 mm, outer side densely covered with erect hairs; stamens c. 1.5 mm long, connective shield papillate to hairy. *Monocarps* 15–30, reddish green in vivo, black in sicco, ellipsoid, 12–15 by 7–8 mm, densely covered with erect hairs, soon sparsely so, apex slightly apiculate (apiculum < 1 mm long), wall c. 1 mm thick, stipes absent. *Seed* ellipsoid, c. 10 by 4 mm, dark brown, apex slighly pointed, rugulose, raphe not distinct from rest of seed.

Distribution — Brazil (Minas Gerais).

Habitat & Ecology — In campo rupestre vegetation, on rocky slopes. At elevations of 950–1300 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Not recorded.

Note — *Guatteria notabilis*, one of the most beautiful species in the genus, cannot be confused with any species in the genus because of the combination of terminal 1–3-flowered inflorescences, densely hairy leaves and flowers, almost sessile monocarps and densely verruculose leaves.

105. *Guatteria novogranatensis* R.E.Fr. — Map 23

Guatteria novogranatensis R.E.Fr. (1939) 496, f. 29a, b; Maas & Westra (2011) 135, f. 18. — Type: *Lawrance 552* (holo S; iso BM, COL, E, F 2 sheets, GH, MO 2 sheets, NY, 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, forming more or less distinct marginal vein, at a smallest distance of 4–7 mm from the margin, tertiary veins inconspicuous and hardly visible, percurrent. *Flowers* on densely branched compact clusters, on the trunk; flowering and fruiting pedicels 35–60 mm long, 2.5–4 mm diam, densely to rather densely covered with appressed hairs, articulated at c. 0.1 from the base, bracts not seen and difficult to count (> 5?); 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 or yellow in vivo, ovate-oblong, 15–25 by 8–13 mm, outer side densely covered with appressed hairs; stamens 2–2.5 mm long, connective shield papillate. *Monocarps* 20–40, colour in vivo not recorded, blackish brown in sicco, ellipsoid, 18–20 by 7–8 mm, glabrous, apex apiculate (apiculum < 1 mm long), wall c. 0.2 mm thick, stipes 8–12 by c. 1 mm. *Seed* ellipsoid, 18–20 by 7–8 mm, dark, shiny brown, longitudinally and transversely grooved, raphe not distinct from rest of seed.

Distribution — Colombia (Boyacá, Santander).

Habitat & Ecology — In non-inundated forest. At elevations of 100–1100 m. Flowering: January, February; fruiting: October.

Vernacular names — Not recorded.

Note — *Guatteria novogranatensis* looks quite similar to the Amazonian species *G. longicuspis*, both being cauliflorous and sharing most leaf characters. *Guatteria 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). It should not be ruled out that future research will prove the two taxa to be conspecific.

106. *Guatteria oblonga* R.E.Fr.

Guatteria oblonga R.E.Fr. (1939) 443, f. 19a, b. — Type: *Melinon s.n.* (holo P; iso B 2 sheets, RB), French Guiana, Maroni River ('Bords de la Rivière du Maroni'), anno 1862.

Tree or shrub of unknown height, diam not recorded; young twigs densely covered with erect, pale brown hairs to c. 1 mm long, soon glabrous. *Leaves*: petiole 4–7 mm long, 1.5–2 mm diam; lamina narrowly elliptic, 10–15 by 3–4.5 cm (leaf index 2.9–3.4), chartaceous, not verruculose, slightly shiny and dark brown above, brown below, glabrous above, primary vein densely covered with appressed to erect, brown hairs below, elsewhere rather densely covered with appressed, brown hairs to c. 1 mm long below, base acute to attenuate, apex acuminate (acumen 5–10 mm long), primary vein flat to slightly impressed above, secondary veins indistinct, 10–12 on either side of primary vein, flat above, smallest distance between loops and margin 1.5–2 mm, tertiary veins inconspicuous, flat above, percurrent

to reticulate. *Flowers* solitary in axils of leaves or perhaps also on leafless branchlets; pedicels 10–13 mm long, c. 1 mm diam, fruiting pedicels to c. 15 mm long, 2 mm diam, densely covered with erect (to appressed), brown hairs, articulated at c. 0.2 from the base, bracts c. 5, soon falling, not seen; flower buds not seen; sepals, only one seen, deltate, 4–5 by 3–4 mm, reflexed, outer side densely covered with erect, brown hairs [fide Fries], petals colour not recorded, elliptic to elliptic-oblong, 10–11 by 4–7 mm, outer side densely covered with erect, brown hairs; stamens not seen [1–1.2 mm long, connective shield papillate, umbonate – fide Fries]. *Monocarps* c. 50, blackish brown in sicco, ellipsoid, 8–9 mm long, c. 5 mm diam, glabrous, apex apiculate (apiculum c. 0.5 mm long), wall 0.1–0.2 mm thick, stipes 15–20 by 0.5–0.7 mm. *Seed* ellipsoid, c. 8 by 4.5 mm, dark brown, pitted, raphe not or slightly raised, distinct from rest of seed.

Distribution — French Guiana, only known from the type collection.

Note — *Guatteria oblonga* is characterized by leaves which are dark-coloured (in sicco) and with inconspicuous tertiary venation on the upper side, a rather dense cover of appressed brown hairs on the lower side and by pitted seeds. It seems to be without direct allies.

107. *Guatteria oblongifolia* Rusby — Plate 5i, 6a; Map 23

Guatteria oblongifolia Rusby (1907) 320; R.E.Fr. (1939) 391. — Type: *Bang 2232* (holo NY; iso F, G, GH, K, MO, US 2 sheets), Bolivia, without locality.

Tree 4–28 m tall, to c. 35 cm diam; young twigs densely covered with erect, brown, long-persisting hairs, finally glabrous. *Leaves*: petiole 4–10 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly oblong-elliptic, sometimes elliptic, rarely narrowly obovate, (6–)9–24 by 2–9 cm (leaf index 2.2–5), coriaceous, not or very rarely verruculose, dull, greyish black, brownish, or greyish above, mostly brown below, rather densely to sparsely covered with appressed to erect hairs to glabrous above, densely to rather densely covered with erect to sometimes appressed, brown hairs below, primary vein keeled or not, permanently densely covered with erect, curly, brown hairs, base acute to obtuse, slightly attenuate, apex acute to acuminate (acumen 5–15 mm long), primary vein impressed to flat above, secondary veins distinct, 10–15 on either side of primary vein, raised above, smallest distance between loops and margin 1–5 mm, tertiary veins raised above, reticulate. *Flowers* in 1(–4)-flowered inflorescences in axils of leaves; flowering and fruiting pedicels 5–40 mm long, 1–3 mm diam, densely to rather densely covered with erect, brown hairs, becoming subglabrous in fruit, articulated at 0.2–0.5 from the base, bracts 5–7, soon falling, broadly to transversely broadly ovate, basal bracts 1–2 mm long, upper ones elliptic to broadly elliptic, 3–8 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–10 by 4–8 mm, reflexed, outer side densely covered with appressed hairs; petals greenish yellow, yellow, cream or red-purple (*Van der Werff 8279*) in vivo, narrowly elliptic, oblong-ovate or ovate, 12–20 by 5–10 mm, outer side densely covered with erect, curly, greyish white to brown hairs; stamens 1.5–2 mm long, connective shield papillate, hairy, or glabrous. *Monocarps* 15–60, green, maturing, brownish red to blackish in vivo, brown to black in sicco, ellipsoid, rarely subglobose, 9–15 by 5–10 mm, rather densely to sparsely covered with appressed and erect hairs, soon glabrous, apex rounded to apiculate (apiculum < 0.5 mm long), wall 0.3–0.7 mm thick, stipes 1–12 by 1–2 mm or absent. *Seed* ellipsoid, rarely subglobose, 10–16 by 5–8 mm, mostly dark, shiny brown, pitted to rugulose, raphe not distinct from rest of seed.

Distribution — Ecuador (Chimborazo, Zamora-Chinchipe), Peru (Cajamarca, Cusco, Pasco, San Martín), Bolivia (La Paz).

Habitat & Ecology — In montane or premontane forest ('bosque yungueño montano pluvial', 'bosque enano', 'bosque semichapparado', low dense forest with sandstone-restricted trees and shrubs), with *Alchornea* sp., *Aniba muca*, *Beilschmiedia tovarensis*, *Clethra* spp., *Clusia* sp., *Cyathea* spp., *Eleagia mariae*, *Graffenrieda emarginata*, *Hedyosmum* sp., *Helicostylis tovarensis*, *Lauraceae* spp., *Miconia* spp., *Nectandra* cf. *laurel* and *Weinmannia* spp., on sandstone soils. At elevations of 1000–2900 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Not recorded.

Notes — *Guatteria oblongifolia* is one of the few species of *Guatteria* which is restricted to high elevations, namely montane and premontane forests of Ecuador, Peru and Bolivia. It is well recognizable by coriaceous leaves, a dense indument of rather long-persisting, erect, brown hairs on the young twigs and lower side of the lamina, and by shortly stipitate or sessile monocarps. The indument on the upper side of the lamina is variable, though, with specimens from the Northern part of the range with the upper side of the lamina being rather densely covered with erect hairs, and those of the Southern part sparsely so to glabrous. As all specimens examined match with each other in general, e.g., flower and fruit features, we favour the concept of one species. For some time we had provisionally indicated it as 'hairy high elevation *Guatteria*', but upon closer look we have concluded that it is identical with Rusby's albeit poorly known concept of *G. oblongifolia*. The type collection by Miguel Bang from Bolivia lacks any precise data. It seems safe to assume that it originated from the department of La Paz, like many recent collections of this species.

Several collections from the Peruvian department of Pasco have densely verruculose leaves, otherwise not known in *G. oblongifolia*. Most other collections from that region look very similar but lack the tiny warts. It is hardly conceivable that the verruculose-leaved specimens belong to a different species; they are best treated as an aberrant form of *G. oblongifolia*. It involves:

Peru, **Pasco**, Oxapampa, Distr. Palcazú, Reserva Comunal Yanesha, Comunidad Nativa San Pedro de Pichanaz, Sector Azulis, 910 m, *Monteagudo M. et al. 9816* (MO); Oxapampa, Distr. Huancabamba, Parque Nacional Yanachaga-Chemillén, Río Chillcatambo, 1800 m, *Monteagudo M. et al. 16588* (L, MO); Oxapampa, Distr. Huancabamba, Parque Nacional Yanachaga-Chemillén, Cajonpata-María Puñis, 1870 m, *Monteagudo M. et al. 16864* (L, MO); Oxapampa, Distr. Huancabamba, Parque Nacional Yanachaga-Chemillén, near house of Orlando Quispe, 1894 m, *Monteagudo M. et al. 16960* (L, MO); Oxapampa, Distr. Palcazú, comunidad Nativa Alto Lagarto, Reserva Comunal Yanesha, 584 m, *Rojas & Ortiz 7029* (L, MO), *7101* (L, MO); Oxapampa, Distr. Huancabamba, Parque Nacional Yanachaga-Chemillén, Sector Tunqui, 1760–1857 m, *Vásquez et al. 33241* (L, MO), *35115* (L, MO), *35125* (L, MO); Oxapampa, Distr. Villa Rica, Sector Ubiriqui, 1537 m, *Vásquez et al. 36042* (L, MO)

108. *Guatteria odorata* R.E.Fr. — Map 23

Guatteria odorata R.E.Fr. (1939) 531, t. 38. — Type: *Ducke MG 15722 = RB 35316* (holo S; iso RB), Brazil, Pará, Óbidos, 16 Mar. 1915.

Tree of unknown height ('arbor parva'), diam not recorded; young twigs densely covered with appressed, brown hairs, soon glabrous. *Leaves*: petiole 2–4 mm long, 0.5–1 mm diam; lamina narrowly elliptic, 5–6 by 1.5–2.5 cm (leaf index 2.5–4), chartaceous, not verruculose, shiny, dark brown above, brown below, glabrous above, but rather densely to sparsely covered with erect hairs mainly along primary vein, rather densely covered with appressed hairs to c. 1 mm long below, base attenuate, apex shortly and bluntly acuminate (acumen to c. 5 mm long), primary vein impressed to flat above, secondary veins distinct, 5–10 on either side of primary vein, raised above, smallest distance between loops and margin 1–3 mm, tertiary veins raised above, reticulate. *Flowers* soli-

Plate 6 a. *Guatteria oblongifolia* Rusby. Fruit. – b, c. *Guatteria oliviformis* Donn. Sm. b. Flowering branch; c. fruit. – d, e. *Guatteria ouregou* (Aubl.) Dunal. d. Part of flowering branch; e. fruit. – f. *Guatteria pichinchae* Maas & Westra. Flowering branch, fruit, two monocarps in ls. – g, h. *Guatteria ramiflora* (D.R.Simpson) Erkens & Maas. g. Flowering branch; h. flowers, detail of g (a: *Neill et al. 15848*; b: *Maas et al. 8001*; c: *Maas et al. 9510*; d, e: *Maas & Maas-van de Kamer 9304*; f: *Cornejo & Montenegro 8355*, type coll.; g, h: *Maas et al. 8270*). — Photos: a: D. Neill; b, c–e, g, h: P.J.M. Maas; f: X. Cornejo.

tary in axils of leaves; pedicels c. 20 mm long, c. 1 mm diam, rather densely to sparsely covered with appressed hairs, articulated at 0.2–0.3 from the base, bracts 5–6, soon falling, not seen; flower buds not seen; sepals free, broadly ovate-triangular, 4–5 by 4–5 mm, soon reflexed, outer side rather densely covered with appressed hairs; petals yellowish in vivo, elliptic to obovate to narrowly so, 15–20 by 5–10 mm, outer side densely covered with appressed and erect, curly hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* and *seed* not seen.

Distribution — Amazonian Brazil (Pará).

Habitat & Ecology — In secondary forest. At an elevation of c. 50 m. Flowering: March; fruiting: unknown.

Vernacular name — Brazil: Envira-preta (*Ducke MG 15722*).

Field observations — Ducke noted down that the flowers of this species are strongly fragrant ('odoratissimis').

Note — *Guatteria odorata* is recognizable by very small leaves (5–6 cm long) covered with long, appressed hairs below, and by small sepals (4–5 mm long). Additional material, particularly of fruits, is necessary to understand its proper position within the genus.

109. *Guatteria oligocarpa* Mart. — Fig. 52; Map 23

Guatteria oligocarpa Mart. (1841) 33; R.E.Fr. (1939) 406. — Type: *Martius 714* (lecto M, selected by Fries 1939; iso B, BM, BR, F, G 2 sheets, HAL, K, L 2 sheets, M 3 sheets, MO, NY, P, S, W), Brazil, Bahia, Ilhéus, Fazenda Almada ('in sylvis primaevis ad Almada'), Dec. 1818.

Guatteria cauliflora Mart. (1841) 35. — *Guatteria bahiensis* R.E.Fr. (1939) 408, f. 10a. — Type: *Blanchet s.n.* (lecto B, selected by Fries 1939; isolecto BR), Brazil, Bahia, without locality.

Tree or shrub 1.5–15 m tall; 13–35 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 5–12 mm long, 2–5 mm diam; lamina narrowly obovate to obovate, 11–25 by 4–12 cm (leaf index 1.7–3.8), subcoriaceous to coriaceous, not verruculose, shiny, brown above, dark brown below, glabrous above, sparsely covered with appressed hairs to glabrous below, base obtuse, apex acute to acuminate (acumen c. 10 mm long), primary vein impressed above, secondary veins indistinct, 10–17 on either side of primary vein, raised above, smallest distance between loops and margin c. 2 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 5–20 mm long, c. 2 mm diam, fruiting pedicels to c. 3 mm diam, sparsely covered with appressed, brown hairs to glabrous, articulated at c. 0.2 from the base, bracts not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 5–7 by 5–8 mm, reflexed, outer side glabrous; petals cream or yellow in vivo, elliptic, 12–20 by 6–11 mm, outer side densely covered with curly hairs to glabrous; stamens c. 2 mm long, connective shield hairy. *Monocarps* 10–35, dark purple in vivo, black to brown in sicco, globose, 12–20 by 10–13 mm, glabrous, apex rounded, wall c. 1 mm thick, stipes 5–30 by 1 mm. *Seed* ellipsoid, c. 10 by 7 mm, brown to dark purple, smooth to slightly pitted, raphe slightly raised.

Distribution — Brazil (Alagoas, Bahia).

Habitat & Ecology — In non-inundated, Atlantic rain forest or periodically inundated forest, on clayey to sandy soil. At elevations of 0–1070 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular name — Brazil: Pindaíba-cabo-de-rodo (*L.A.M. Silva et al. 2463*).

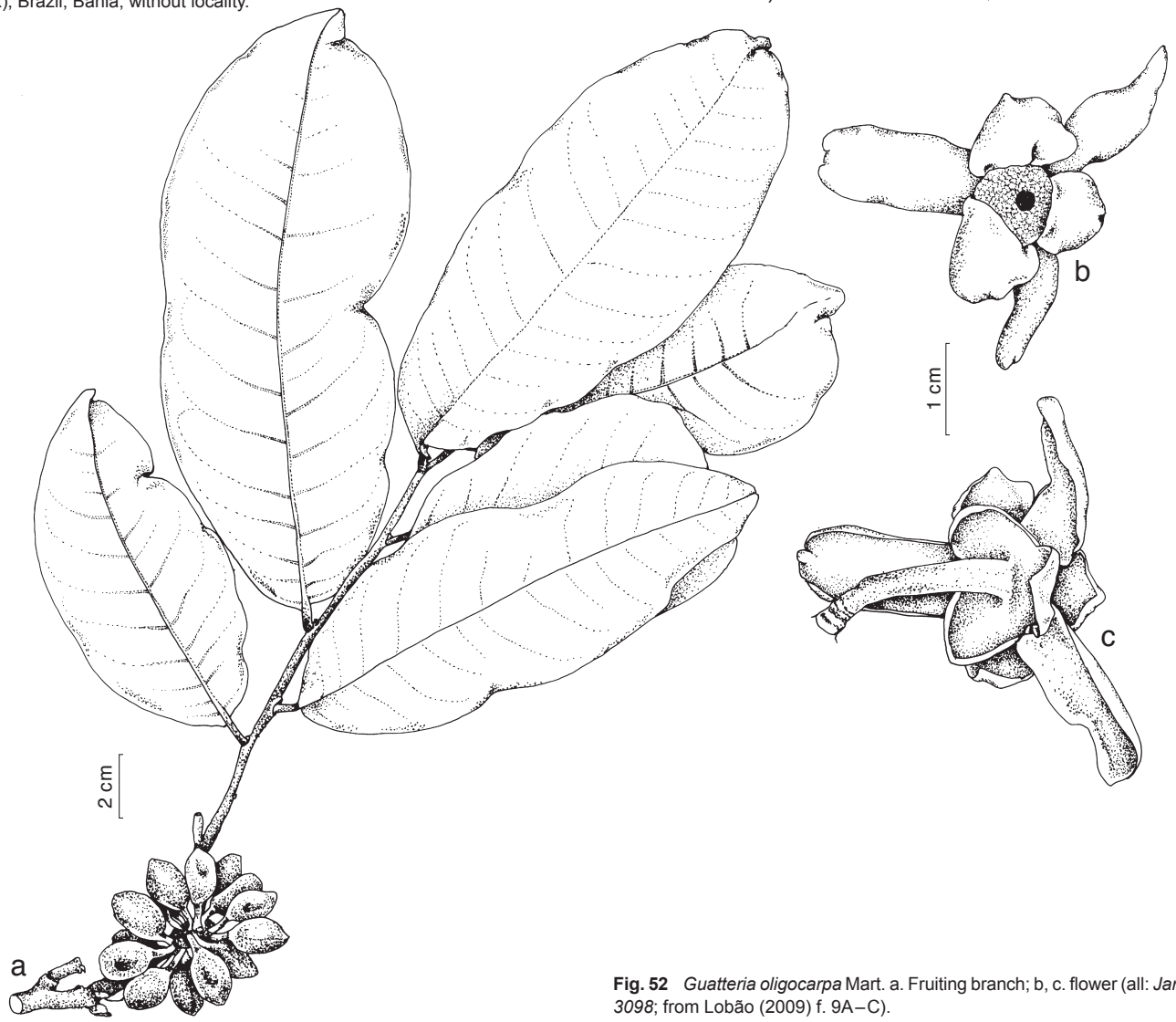


Fig. 52 *Guatteria oligocarpa* Mart. a. Fruiting branch; b, c. flower (all: *Jardim 3098*; from Lobão (2009) f. 9A–C).

Note — *Guatteria oligocarpa* is characterized by medium-sized to large, subcoriaceous to coriaceous leaves, and globose monocarps and seeds not adhering to the monocarp wall in sicco. Vegetative plants of *G. oligocarpa* may have larger leaves than just decribed, and then resemble *G. pogonopus*, but the latter has ellipsoid instead of globose monocarps, and seeds remain stuck to the monocarp wall in sicco.

110. *Guatteria oliviformis* Donn.Sm. — Plate 6b, c; Map 25

Guatteria oliviformis Donn.Sm. (1897) 1; R.E.Fr. (1939) 521, f. 35b–f. — Type: *Tonduz 1740* (lecto BR, selected by Fries 1939; isolecto CR, US), Costa Rica, Heredia, Volcán Barba, Río Segundo, 2000 m, 10 Jan. 1890.

Tree 5–25 m tall, 10–50 cm diam; young twigs often zigzagging, densely covered with long-persisting, erect, brown hairs. *Leaves*: petiole 3–7 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly obovate, 10–20 by 3–7 cm (leaf index 3–3.3), coriaceous to slightly chartaceous, rather densely to densely verruculose, dull, blueish green above, brown below, densely covered with erect, brown hairs along the primary vein above, becoming glabrous, densely covered with erect, brown hairs below, base acute to obtuse, apex acuminate (acumen 5–15 mm long), primary vein impressed to slightly raised above, secondary veins distinct, 8–12 on either side of primary vein, slightly raised above, smallest distance between loops and margin 1–2 mm, tertiary veins inconspicuous, flat to slightly raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; pedicels 7–25 mm long, c. 1 mm diam, fruiting pedicels 30–40 mm long, c. 3 mm diam, densely to sparsely covered with erect, brown hairs, articulated at 0.2–0.5 from the base, bracts 5–7, soon falling, very rarely foliaceous and elliptic, to c. 60 mm long; flower buds depressed ovoid; sepals free, very broadly to shallowly ovate-triangular, 5–7 by 5–9 mm, reflexed, outer side rather densely to sparsely covered with appressed, whitish hairs; petals yellowish green or yellow in vivo, ovate to elliptic, 12–16{–25} by 7–10{–15} mm, outer side densely covered with appressed and erect, whitish hairs; stamens 2–2.5 mm long, connective shield papillate. *Monocarps* 10–50, maturing purplish black in vivo, black in sicco, ellipsoid, 9–16 by 6–11 mm, somewhat wrinkled, glabrous, apex rounded to apiculate (apiculum < 0.5 mm long), wall c. 0.5 mm thick, stipes 3–7 by 1–2 mm. *Seed* ellipsoid, 9–12 by 6–7 mm, dark brown, rugose, raphe not distinct from rest of seed.

Distribution — Costa Rica, Panama.

Habitat & Ecology — In low, montane cloud forest. At elevations of (0–)700–2200 m. Flowering: throughout the year; fruiting: February, May, September to November.

Vernacular name — Costa Rica: Anonillo (*Tonduz 1740*).

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

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

111. *Guatteria oriximinae* Maas & Westra, *sp. nov.* — Fig. 53, 54a; Map 25

Species praecipue sepalis parvis extus rugulosis et pilis adpressis parce (nec dense) obtectis, praetera foliis coriaceis, monocarpiis breviter stipitatis distincta. — Typus: *Campbell et al. P 22316* (holo U; iso INPA, L, NY), Brazil, Pará, junction of Rio Trombetas and Rio Mapuera, 30 May 1974.

Erect or scandent shrub or tree 4–8 m tall, diam not recorded; young twigs sparsely covered with appressed hairs to glabrous. *Leaves*: petiole 5–10 mm long, 1–2 mm diam; lamina narrowly elliptic to elliptic, 8–14 by 3–6.5 cm (leaf index 2.1–2.7), coriaceous, not verruculose, slightly shiny to dull, greyish green to greyish brown above, brown below, glabrous above, sparsely covered with appressed hairs (mainly along primary vein) to glabrous below, base acute to obtuse, extreme base mostly attenuate, apex acute to bluntly acuminate (acumen to c. 10 mm long), primary vein impressed above, secondary veins distinct, 8–12 on either side of primary vein, impressed above, smallest distance between loops and margin 4–5 mm, tertiary veins inconspicuous, flat above, percurrent to reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 8–11 mm long, 1–1.5 mm diam, fruiting pedicels to c. 2 mm diam, subglabrous, articulated at 0.3–0.4 from the base, bracts 5–6, soon falling, only 1 basal bract seen, very broadly ovate, c. 1 mm long; flower buds depressed ovoid; sepals free, shallowly ovate-triangular, 2.5–3 by 3–5 mm, spreading, outer side sparsely covered with appressed hairs, rugulose; petals green, maturing yellow in vivo, narrowly elliptic, 10–15 by 4–5 mm, outer side densely covered with appressed, greyish white hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* 5–50, green when young in vivo, black in sicco, ellipsoid to narrowly ellipsoid, 10–12 by 4–5 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 0.2 mm long), wall 0.1–0.2 mm thick, stipes 5–10 by c. 1 mm. *Seed* ellipsoid to narrowly ellipsoid, 10–12 by c. 4 mm, brown, rugose, raphe not distinct from rest of seed.

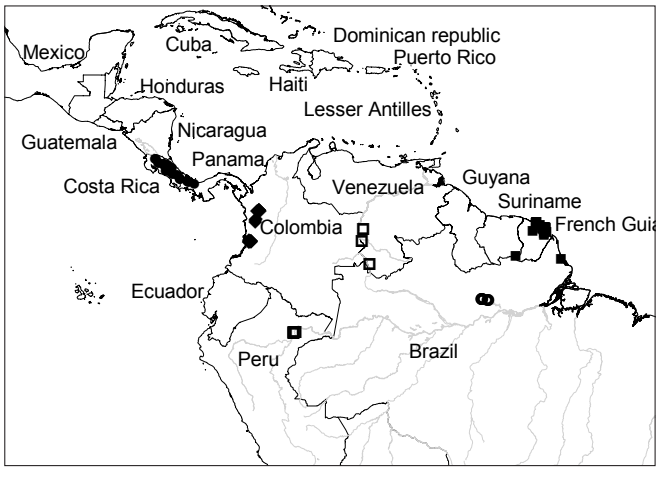
Distribution — Amazonian Brazil (Pará).

Habitat & Ecology — In periodically inundated forest or sandy beach, on sandy to rocky soil ('solo arenoso-pedregoso'). At elevations of about sea level. Flowering: May, July, August; fruiting: November.

Vernacular names — Not recorded.

Other specimens examined. Brazil, **Pará**, Mun. Oriximiná, Rio Trombetas, island in front of 'Acampamento da Gutierrez', 2 July 1980, *Cid et al. 1236* (MO, NY, U); Mun. Oriximiná, right bank of Rio Mapuera, between Cachoeira Paraíso Grande and Maracajá, 12 Aug. 1982, *Cid et al. 7671* (NY, U), *7679* (NY, U); idem, 13 Aug. 1986, *Cid et al. 7694* (NY, U); Mun. Oriximiná, area of future hydroelectric usina de Cachoeira Porteira, near Cachoeira Viramundo, 23 Nov. 1987, *Cid et al. 9654* (NY, U); Mun. Oriximiná, Cachoeira Porteira, on rocky outcrop, at margin of Porto de Índio, 18 Nov. 1987, *Farney et al. 1941* (NY, U).

Note — *Guatteria oriximinae* is a narrow endemic mainly restricted to the Mun. Oriximiná in the Brazilian state of Pará. It can at first glance be recognized by a combination of shortly stipitate monocarps (stipes shorter than the monocarps) and very small sepals (to 3 mm long), which, moreover, are rugulose



Map 25 Distribution of *Guatteria oliviformis* (●), *G. oriximinae* (⭘), *G. ouregou* (■), *G. pachyphylla* (□) and *G. pacifica* (◆).

Fig. 53 *Guatteria oriximinae* Maas & Westra. Flowering branch (*Campbell et al. P22316*, holotype U).

Fig. 54 a. *Guatteria oriximinae* Maas & Westra. Fruit. – b. *Guatteria pachycarpa* Erkens & N.Zamora. Monocarp in cross section. – c, d. *Guatteria paludosa* R.E.Fr. c. Flowers; d. flower buds and bracts. – e. *Guatteria procera* R.E.Fr. Fruit. – f. *Guatteria revoluta* Maas & Westra. Rvolute leaf base, fruit and incomplete flower. – g. *Guatteria rigida* R.E.Fr. Fruit. – h. *Guatteria ruboides* Maas & Westra. Fruit (a: *Cid et al. 9654*, U; b: *G. Herrera C. 5227*, U; c, d: *McDowell et al. 4815*, U; e: *Sperling et al. 6227*, U; f: *Vásquez & Jaramillo 8024*, isotype U [sheet 2]; g: *Anderson et al. 106*, U; h: *Vásquez & Jaramillo 8025*, isotype AAU).

Fig. 55 *Guatteria pachycarpa* Erkens & N.Zamora. Branch and (separate) fertile parts (*G. Herrera C. 5227*, isotype U).

on the outer side. The latter feature is not known in any other *Guatteria* species. It is one of the few species of *Guatteria* that occur in periodically inundated forests. Furthermore it is growing on sandy-rocky soils near water falls. Its relationships needs additional study.

112. *Guatteria ouregou* (Aubl.) Dunal — Plate 6d, e; Map 25

Guatteria ouregou (Aubl.) Dunal (1817) 126; R.E.Fr. (1939) 352, f. 7, t. 20. — *Cananga ouregou* Aubl. (1775) 608, t. 244. — *Uvaria monosperma* Lam. (1785) 596. — Type: *Aublet's table 244* (lecto, here selected), French Guiana, Sinnamary ('in sylvis remotis Sinemariensibus'), as no herbarium material attributable to Aublet could be traced.

Unona crassipetala Dunal (1817) 101, t. 24. — *Unona pachypetala* Spreng. (1825) 637. — Type: *Anonymous collector s.n.* (holo G), French Guiana, without location.

Unona fuscata DC. ex Dunal (1817) 102. — Type: *Martin s.n.* (holo G; iso BM), French Guiana, without location.

Guatteria podocarpa DC. ex Dunal (1817) 127. — *Guatteria podocarpa* DC. ex Dunal var. *oligocarpa* DC. (1817) 503. — Type: *Anonymous collector s.n.* (holo G), French Guiana ('Cayennà'), without location.

Guatteria podocarpa DC. ex Dunal var. *polycarpa* DC. (1817) 503. — Type: *Anonymous collector s.n.* (holo G), French Guiana ('Cayennà'), without location.

Guatteria ouregou (Aubl.) Dunal var. *latifolia* Sagot (1881) 138. — Type: not seen.

Tree 2–10(–15) m tall, 2.5–15 cm diam; young twigs densely covered with erect, dark brown hairs to c. 2 mm long, soon glabrous. *Leaves*: petiole 3–6 mm long, 1–3 mm diam; lamina narrowly elliptic, 14–28 by 4–8 cm (leaf index 2.3–3.5), chartaceous, not verruculose, dull, brownish, sometimes greyish above, brown below, glabrous above, except for some hairs along primary vein, rather densely covered with erect, dark brown hairs below, soon becoming glabrous, except for primary and secondary veins, base obtuse, sometimes acute, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins distinct, 11–15 on either side of primary vein, impressed above, smallest distance between loops and margin 3–5 mm, tertiary veins flat to slightly raised above, percurrent to reticulate. *Flowers* in 1(–3)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–20 mm long, 1–1.5 mm diam, fruiting pedicels 15–25 mm long, 1.5–3.5 mm diam, densely covered with erect, dark brown hairs to c. 2 mm long, articulated at 0.2–0.5 from the base, bracts 4–6, soon falling, the lowermost bract very broadly to transversely ovate, 1–1.5 mm long, the middle one (only one seen) elliptic, c. 2 mm long, uppermost bract not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 6–10 by 5–8 mm, finally reflexed, outer side verruculose, densely covered with erect, dark brown hairs to c. 2 mm long, soon becoming sparsely hairy; petals orange or yellow-orange in vivo, oblong-elliptic to narrowly triangular, 15–35 by 6–12 mm, outer side densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 20–40, green, maturing wine-red to black in vivo, black in sicco, ellipsoid, 8–15 by 5–10{–14} mm, subglabrous, apex rounded to slightly apiculate (apiculum < 1 mm long), wall 0.3–0.6 mm thick, stipes 15–35 by c. 1 mm. *Seed* ellipsoid, 8–10 by 5–6 mm, dark brown, pitted to transversely grooved, raphe not distinct from rest of seed.

Distribution — French Guiana.

Habitat & Ecology — In non-inundated, primary or secondary forest, on lateritic to sandy soil. At elevations of 0–200 m. Flowering: September to March; fruiting: September to February.

Vernacular names — French Guiana: Corossol sauvage (Creole name), Ïwi (Wayãpi name), Kiriksau (Palikur name) (*Grenand 2079*), Mamanyaoué (Creole name), Mamanyaoui (Creole name) (*BAFOG 1051*), Mamayawé (Creole name), Ouregou (Carib name; Aublet (1775): 'Cet arbre est nommé OUREGOU par les Galibis').

Note — *Guatteria ouregou* is a species apparently endemic to French Guiana; it can immediately be recognized by the combination of brown, erect hairs on most of its vegetative parts, relatively large monocarps and orange to yellow-orange petals.

113. *Guatteria pachycarpa* Erkens & N.Zamora, *sp. nov.* — Fig. 54b, 55; Map 19

Monocarpiis pariete crassimisa, breviter stipitatis, praeterea foliis petiolis longissimis basi longe attenuatis ab omnibus speciebus *Guatteriae* distincta. — Typus: *G. Herrera C. 5227* (holo INB; iso MO, U), Costa Rica, Limón, Cantón de Talamanca, Bratsi, Amubri, Alto Lari, Kivut, 1300 m, 8 March 1992 (fl, fr).

Guatteria sp. 1 Erkens (2007) 208.

Tree 15–16 m tall, c. 35 cm diam; young twigs densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 10–18 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly obovate, 5–14 by 3–5.5 cm (leaf index 2.3–2.6), chartaceous, not verruculose, dull, dark brown above, brown below, glabrous above, sparsely covered with appressed hairs, soon glabrous below, base long-attenuate, basal margins slightly revolute, apex acuminate (acumen 5–10 mm long) to acute, primary vein slightly raised above, secondary veins distinct, 10–17 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels c. 10 mm long, c. 1 mm diam, fruiting pedicels 15–20 mm long, c. 3 mm diam, sparsely covered with appressed hairs, articulated at c. 0.3 from the base, bracts 5–7, soon falling, not seen; flower buds depressed ovoid; sepals free, depressed ovate, 3–4 by 4–5 mm, reflexed, outer side rather densely covered with appressed hairs; petals green to cream in vivo, ovate, 7–10 by 4–7 mm, outer side densely covered with appressed hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* 10–15, green, maturing purplish red in vivo, black in sicco, globose, 20–25 mm diam, glabrous, apex rounded, wall 5–6 mm thick, stipes 1.5–2 by 2.5–3 mm. *Seed* narrowly ellipsoid, 9–10 by 3–5 mm, dark brown, rugose, raphe not seen.

Distribution — Costa Rica (Limón).

Habitat & Ecology — In non-inundated, wet forest ('bosque muy húmedo'). At elevations of 1300–1500 m. Flowering: March; fruiting: March.

Vernacular names — Not recorded.

Other specimens examined. Costa Rica, **Limón**, Cantón de Talamanca, Bratsi, Alto Lari, Kivut, 1300–1500 m, 15 Mar. 1992 (fl), *Aguilar & Schmidt 1121* (INB, MO).

Note — *Guatteria pachycarpa* is very aberrant from any other species of *Guatteria* by its very thick monocarp wall (up to 6 mm thick) and also by its very short and thick stipes. The thick monocarp wall of this species appears so inflated that we wondered if the fruit might be galled. However, it is known from two different (nearby) localities in Limón, Costa Rica (*Aguilar & Schmidt 1121*, *Herrera C. 5227*) and on both localities this aberrant fruit type has been found. Another typical feature of this species is its long-attenuate leaves and long petioles (up to 18 mm long).

114. *Guatteria pachyphylla* Maas & Westra — Map 25

Guatteria pachyphylla Maas & Westra (2010) 269, f. 8. — Type: *Vásquez et al. 465* (holo MO; iso NY, U), Peru, Loreto, Prov. Maynas, Puerto Almendras, Río Nanay, above Iquitos, 120 m, 22 Aug. 1980.

Tree 10–24 m tall, diam not recorded; young twigs glabrous. *Leaves*: petiole 6–15 mm long, 1–3 mm diam; lamina narrowly obovate, 10–21 by 3–7 cm (leaf index 2.4–3.3), coriaceous, not verruculose, brown above and below, glabrous on both sides, base attenuate, basal margins slightly revolute, apex shortly and

bluntly acuminate (acumen 1–4 mm long) or obtuse, primary vein impressed above, sharply keeled below, secondary veins indistinct, 12–15 on either side of primary vein, flat to slightly impressed above, smallest distance between loops and margin 3–4 mm, tertiary veins flat to impressed above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 15–20 mm long, c. 1 mm diam, fruiting pedicels 20–25 mm long, c. 2 mm diam, glabrous, articulated at 0.1–0.2 from the base, bracts 5–7, soon falling, uppermost bracts c. 3 by 2 mm; flower buds broadly ovoid; sepals basally connate, shallowly ovate-triangular, 4–5 by 6–7 mm, spreading, but apically reflexed, outer side glabrous, but apex densely covered with curly hairs; petals white or yellow in vivo, narrowly oblong-elliptic, 11–20 by 4–6 mm, outer side rather densely to sparsely covered with crisped, erect hairs; stamens c. 1 mm long, connective shield glabrous. *Monocarps* 10–25, colour in vivo not recorded, black in sicco, narrowly ellipsoid, 12–16 by 4–6 mm, glabrous, apex distinctly pointed (apiculum c. 1 mm long), wall c. 0.2 mm thick, stipes 4–8 by 1 mm. *Seed* narrowly ellipsoid, 12–14 by 4–6 mm, shiny black, rugulose, longitudinally grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Venezuela (Amazonas), Peru (Loreto).

Habitat & Ecology — In non-inundated or periodically inundated forest, on clayey to sandy soil. At elevations of up to 120 m. Flowering: August, September; fruiting: January.

Vernacular names — Not recorded.

Note — *Guatteria pachyphylla* is one of the most distinctive species in *Guatteria* because of its *Clusia*-like, coriaceous, narrowly obovate leaves which have a shortly acuminate apex (acumen 1–4 mm long) and impressed tertiary veins. Moreover, the monocarps are distinctly and sharply pointed. It looks superficially similar to the rarely collected Guyanan species *G. clusiifolia*, sharing most leaf characters, but from that species it differs by much smaller monocarps (12–16 vs c. 22 mm long). Moreover, the monocarps of *G. clusiifolia* have an obtuse apex and are not sharply pointed as in *G. pachyphylla*.

115. *Guatteria pacifica* R.E.Fr. — Fig. 56; Map 25

Guatteria pacifica R.E.Fr. (1950a) 337. — Type: *Cuatrecasas 17150* (holo S 2 sheets; iso COL 2 sheets, F 2 sheets, L, S, US 2 sheets), Colombia, Valle del Cauca, Costa del Pacífico, Río Cajambre, Barco, 5–80 m, 21–30 Apr. 1944.

Tree 6–30 m tall, 6–50 cm diam; young twigs sparsely covered with appressed, brown hairs, soon glabrous. *Leaves*: petiole 7–20 mm long, 3–4 mm diam, winged; lamina narrowly obovate to obovate, 15–34 by 6–13 cm (leaf index 2–2.9), coriaceous, densely verruculose, dull, dark brownish above, pale brown below, glabrous above, sparsely covered with appressed, brown hairs to glabrous below, base acute to attenuate, apex acuminate (acumen 5–15 mm long), primary vein impressed above, keeled below, secondary veins distinct, 11–20 on either side of primary vein, flat to slightly impressed above, smallest distance between loops and margin 2–4 mm, tertiary veins flat to slightly impressed above, reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; pedicels 15–50 mm long, 1.5–2 mm diam, fruiting pedicels to c. 3 mm diam, sparsely covered with appressed, brown hairs, articulated at 0.2–0.5 from the base, bracts 5–6, soon falling, the 2 upper ones 13–14 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–6 by 4–5 mm, appressed, outer side rather densely covered with appressed, brown hairs, densely so at the apex; petals green, pale green, cream or pale yellow in vivo, ovate to obovate, 11–30 by 7–15 mm, outer side densely covered with appressed, brown hairs; stamens c. 2 mm long, connective shield papillate, umbonate. *Monocarps* 10–35, green, maturing purple-black in vivo, brownish in sicco, narrowly ellipsoid, 13–20 by 4–8{–10} mm, sparsely covered with appressed, brown hairs, soon glabrous, apex apiculate (apiculum 0.5–1 mm long), wall 0.2–0.3 mm thick, stipes 4–10 by 1–2 mm. *Seed* narrowly ellipsoid to ellipsoid, 12–17 by 4–6 mm, shiny, reddish brown, pitted to transversely grooved, raphe raised to flat.

Distribution — Pacific coast of Colombia (Antioquia, Chocó, Valle del Cauca).

Habitat & Ecology — In primary or secondary rain forests or in premontane forests (Antioquia), along margins of rivers and creeks, on yellow clay or yellowish grey clayey loam. At elevations of 0–1450 m. Flowering: January, April to August, October; fruiting: April, July to October.

Vernacular names — Colombia: Cargadero (*Cogollo et al. 3625*, *Faber-Langendoen et al. 889*), Rayado (*Faber-Langendoen et al. 1050*).

Notes — *Guatteria pacifica* can be recognized by a combination of leaves densely verruculose on both sides (even visible by the naked eye), a primary vein keeled on the lower side of the lamina and long-pedicellate flowers.

Some material collected in the Colombian department of Antioquia (*Cogollo et al. 3310*, *D.A. Sánchez S. et al. 271*) is aberrant in having large monocarps (c. 20 by 10 mm) with longer stipes (to 14 mm long).

116. *Guatteria pakaraimae* Scharf & Maas — Map 22

Guatteria pakaraimae Scharf & Maas in Scharf et al. (2005) 568, f. 3; Maas & Westra (2011) 137. — Type: *Henkel et al. 4279* (holo NY; iso BRG, CAY, U, US), Guyana, Pakaraima Mts, W slope on subplateau near head of Mo-toy-mabaru 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 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 slightly raised above, reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; 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 free, broadly ovate-triangular, c. 3 by 3–4 mm, appressed, outer side subglabrous; petals green in vivo, ovate-oblong, 10–12 by c. 5 mm, outer base densely covered with appressed hairs, towards the apex sparsely covered with curly hairs; stamens c. 2 mm long, connective shield 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 c. 2 mm. *Seed* ellipsoid, 12–13 by 6–7 mm, shiny, reddish brown, rugulose, raphe not distinct from rest of seed.

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*, *Melastomataceae*, *Moronobea*). At elevations of 1135–1200 m. Flowering: November; fruiting: July.

Vernacular names — Not recorded.

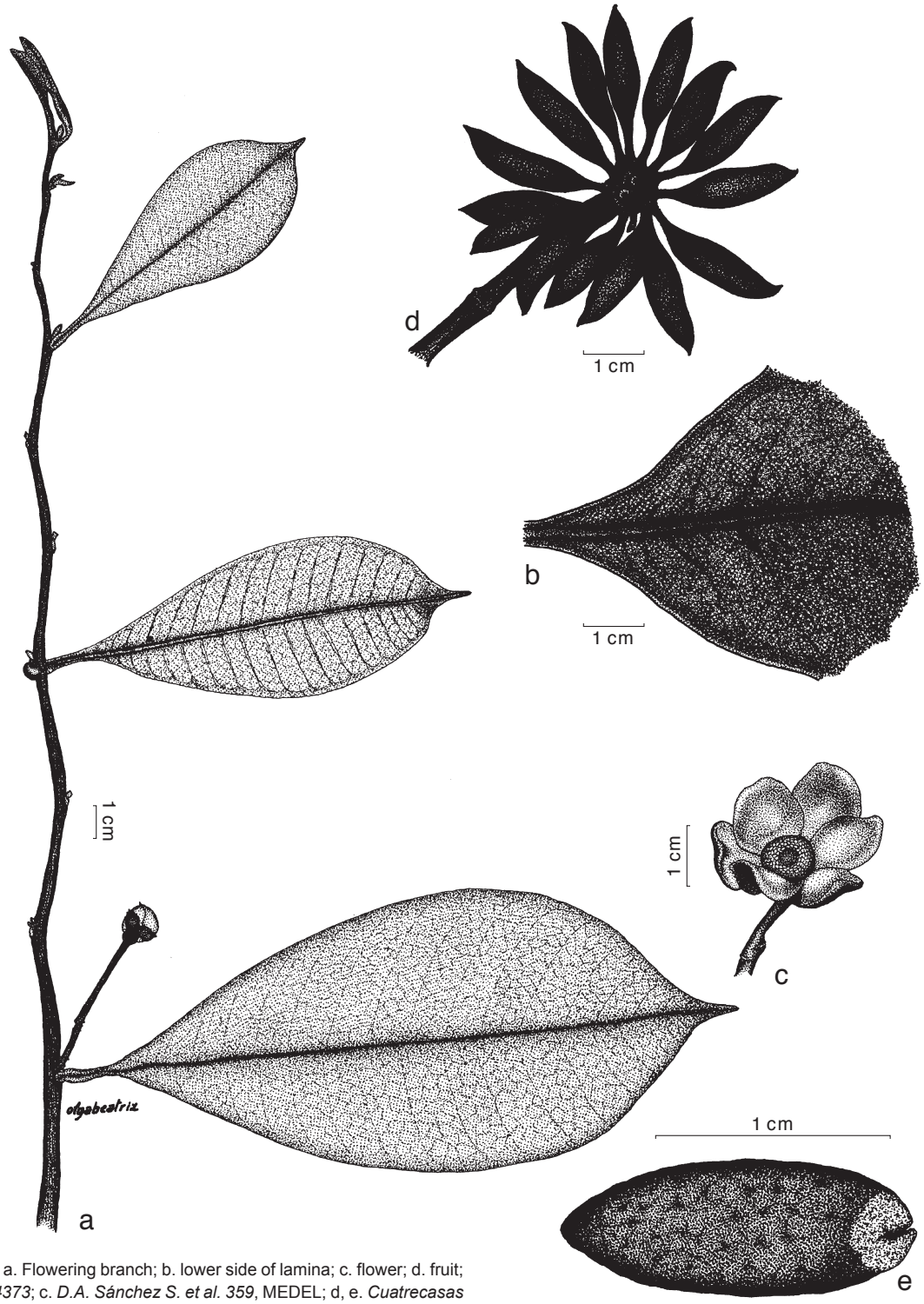


Fig. 56 *Guatteria pacifica* R.E.Fr. a. Flowering branch; b. lower side of lamina; c. flower; d. fruit; e. seed (a, b. *Gentry & Rentería 24373*; c. *D.A. Sánchez S. et al. 359*, MEDEL; d, e. *Cuatrecasas 17150*, isotype COL; from Sánchez S. (1986) f. 4).

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

117. *Guatteria paludosa* R.E.Fr. — Fig. 54c, d, 57; Map 26

Guatteria paludosa R.E.Fr. (1948a) 231. — Type: *Forest Department British Guiana 3781 = Fanshawe 1045* (holo K 2 sheets; iso FDG, NY), Guyana, Mahdia River, Potaro River, miles 107 of Bartica-Potaro Road, common by creeks in Kataburi (*Rapatea*) swamp, 18 Jan. 1943.

Tree 8–25 m tall, 15–50 cm diam; young twigs densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 15–30 mm long, 3–4 mm diam, strongly thickened at the base; lamina narrowly elliptic, 32–53 by 8–14 cm (leaf index 2.4–3.7), chartaceous, scabridulous, greyish brown above, brown below, glabrous on both sides, base long-attenuate, apex acuminate (acumen 10–45 mm long), primary vein impressed above, secondary veins distinct, 15–27 on either side of primary vein, impressed above, smallest distance between loops and margin 2–3 mm, tertiary veins inconspicuous, flat above, reticulate to percurrent. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 5–15 mm long, c. 1 mm diam, fruiting pedicels to c. 3 mm diam, densely covered with appressed hairs, articulated at 0.2–0.3 from the base, bracts 5–6, soon falling or rarely present before anthesis, elliptic to

Fig. 57 *Guatteria paludosa* R.E.Fr. Fruiting habit (*Redden et al. 2243*, U).

Map 26 Distribution of *Guatteria paludosa* (●), *G. pastazae* (⊙), *G. peruviana* (■), *G. pittieri* (□) and *G. pogonopus* (◆).

narrowly elliptic, 7–13 mm long; flower buds depressed ovoid, slightly pointed; sepals free, broadly to shallowly ovate-triangular, 5–7 by 7–10 mm, reflexed, outer side densely covered with appressed hairs; petals yellow or cream in vivo, oblong-obovate, 15–40 by 7–16 mm, outer side densely covered with appressed hairs; stamens 2–3 mm long, connective shield papillate to hairy. *Monocarps* 10–30, green, maturing purple-black in vivo, black in sicco, ellipsoid, 18–20 by 10–11 mm, glabrous, apex apiculate (apiculum broadly conical, hard, < 1 mm long), wall c. 0.5 mm thick, stipes 5–8 by 1.5–2 mm. *Seed* ellipsoid, 14–17 by 9–10 mm, red-brown, rugulose, raphe not distinct from rest of seed.

Distribution — Guyana.

Habitat & Ecology — In non-inundated, mixed rain forest, usually along creeks, sometimes on steep hills, on lateritic soil. At elevations of 0–600 m. Flowering: May, June; fruiting: January, March, June, October.

Vernacular name — Guyana: Smooth skin arara (Arawak name).

Notes — *Guatteria paludosa*, a narrow endemic of Guyana, looks superficially like a member of sect. *Mecocarpus* (where it was also placed by Fries 1948a), but the leaves are scabridulous rather than verruculose.

For the differences with *G. anteridifera*, a species occurring in French Guiana and the adjacent Brazilian state of Amapá, see under that species.

118. *Guatteria panamensis* (R.E.Fr.) R.E.Fr. — Map 22

Guatteria panamensis (R.E.Fr.) R.E.Fr. (1950a) 335. — *Guatteria costaricensis* R.E.Fr. subsp. *panamensis* R.E.Fr. (1939) 515. — Type: *Cooper 382* (holo F; iso K, US), Panama, Bocas del Toro, region of Almirante, Daytonia Farm, 1 Dec. 1928.

Tree 6–13 m tall, diam not recorded; young twigs rather densely to densely covered with appressed hairs. *Leaves*: petiole 3–7 mm long, 1–2 mm diam; lamina narrowly obovate to narrowly elliptic, 13–27 by 5–12 cm (leaf index 1.8–3), chartaceous, not verruculose, dull, greyish black above, greenish brown below, glabrous above, densely to rather densely covered with appressed hairs on primary and secondary veins, otherwise sparsely so to glabrous below, base acute, apex acuminate (acumen 5–10 mm long), primary vein flat above, secondary veins distinct, 15–18 on either side of primary vein, flat to slightly raised above, smallest distance between loops and margin 1–3 mm, tertiary veins indistinct, flat to slightly raised above, reticulate to slightly percurrent. *Flowers* 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; flowering and fruiting pedicels 20–40 mm long, 1–2 mm diam, rather densely covered with appressed hairs, articulated at c. 0.2 from the base, bracts 5–6, soon falling, not seen; sepals shallowly ovate-triangular, 3–4 by 4–6 mm, appressed to reflexed, outer side densely covered with appressed hairs; petals yellowish green or deep yellow in vivo, ovate to broadly elliptic, 6–17 by 7–10 mm, outer side densely covered with appressed hairs; stamens 1–2 mm long, connective shield papillate. *Monocarps* 30–50, green in vivo, black in sicco, ellipsoid, 7–10 by 3–4 mm (immature), sparsely covered with appressed hairs, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 6–10 by 1 mm. *Seed* ellipsoid, 7–9 by 3–5 mm, dark brown, rugose, raphe slightly impressed.

Distribution — Costa Rica, Panama.

Habitat & Ecology — In non-inundated forest. At elevations of 0–700 m. Flowering: February, November; fruiting: July, December.

Vernacular names — Not recorded.

Note — *Guatteria panamensis* has been poorly collected. It resembles *G. aeruginosa* with which it occurs sympatrically in Panama. However, the latter is distinct by erect hairs on the primary vein on the upper side and on the lower side of the leaf, and mostly has verruculose leaves.

119. *Guatteria pannosa* Scharf & Maas — Map 22

Guatteria pannosa Scharf & Maas in Scharf et al. (2006a) 125, f. 5. — Type: *Barrier & Feuillet 2633* (holo CAY; iso K 2 sheets, NY, P, U, US), French Guiana, Approuague River, Arataye River, Sauts Pararé, 12 Feb. 1981.

Tree 4–25 m tall, over c. 8 cm diam; young twigs densely covered with erect, curly, brown, long-persistent hairs. *Leaves*: petiole 6–8 mm long, 1–2 mm diam; lamina narrowly oblong-elliptic, rarely elliptic, 10–20 by 2.5–5 cm (leaf index 3.2–4), coriaceous, not verruculose, greyish green above, pale brown below, glabrous above, but primary vein with some wavy hairs, densely covered with appressed, brown to white hairs below, base acute, apex acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 10–15 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorscences in axils of leaves or on leafless branchlets; pedicels 8–10 mm long, c. 1 mm diam, fruiting pedicels to c. 15 mm long, c. 3 mm diam, densely covered with a velutinous indument of erect, curly, brown hairs, to subglabrous, articulated at 0.3–0.5 from the base, bracts not seen and not counted; flower buds depressed ovoid, distinctly pointed; sepals free, ovate-triangular, 8–10 by 5–6 mm, appressed to spreading, outer side densely covered with a velutinous indument of erect, curly, reddish brown hairs; petals greenish red in vivo, narrowly triangular, 20–25 by 6–8 mm, outer side densely covered with a velutinous indument of erect, curly, reddish brown hairs, margins reflexed; stamens c. 1 mm long, connective shield papillate. *Monocarps* 25–30, blackish green to black in vivo, dark to rusty brown in sicco, ellipsoid, 10–14 by 6–7 mm, densely covered with erect, curly, brown hairs, soon sparsely so, apex apiculate (apiculum < 0.3 mm long), wall 0.5–1 mm thick, stipes 20–25 by c. 1 mm. *Seed* ellipsoid, 11–13 by 5–6 mm, shiny, reddish brown, smooth to pitted, raphe slightly raised.

Distribution — French Guiana, Amazonian Brazil (Amapá).

Habitat & Ecology — In non-inundated forest. At about sea level. Flowering: February, November; fruiting: August to October.

Vernacular names — French Guiana: Bako pao (Saramaccan, Boni name) (*Villiers & Feuillet 1790*), Pandiecou (*Barrier 3865*).

Note — *Guatteria pannosa* is quite distinctive by having relatively narrow and coriaceous leaves, pointed flower buds, and a felt-like indument of small, appressed hairs (hence the species name 'pannosa') on various parts of the plant. With *G. discolor*, a species occurring in Amazonian Bolivia, Brazil, Peru and French Guiana, it shares the pointed flower buds, differing by smaller monocarps (10–14 vs 15–30 mm long), longer stipes (20–25 vs 2–10 mm), and an indument of small, appressed instead of erect and curly hairs on the lower side of the lamina. It also shares a number of features with the Panamanian species *G. aberrans* (Erkens et al. (2006)), differring, however, by much narrower leaves (2.5–5 vs 4–9.5 cm) and longer stipes (20–25 vs 9–14 mm).

120. *Guatteria partangensis* Scharf & Maas — Map 22

Guatteria partangensis Scharf & Maas in Scharf et al. (2005) 569, f. 4. — Type: *Tillett et al. 43975* (holo K; iso BRG, MO, NY, S, US), Guyana, Merume Mts, Partang River, 3 July 1960.

Tree c. 8 m tall, diam not recorded; young twigs densely covered with erect, long-persisting hairs 1–1.5 mm long. *Leaves*: petiole 3–5 mm long, c. 2 mm diam; lamina narrowly elliptic, 8–15 by 4–5 cm (leaf index 2.8–3.2), coriaceous, not verruculose, dull, greyish brown above, dark to yellowish brown below, glabrous above, but primary vein covered with a dense row of hairs, soon glabrous, rather densely covered with erect hairs c. 1 mm long below, base obtuse, apex acuminate (acumen 10–25 mm long), primary vein impressed above, secondary veins distinct, 6–9 on either side of primary vein, raised above, smallest distance between loops and margin c. 1 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; pedicels c. 40 mm long, c. 1 mm diam, fruiting pedicels c. 50 mm long, 1–1.5 mm diam, densely covered with erect hairs c. 1 mm long, articulated at 0.2–0.4 from the base, bracts 4–5, soon falling, not seen; flower buds not seen; sepals free, broadly ovate-triangular, 5–7 by 5–7 mm, appressed, outer side densely covered with erect hairs; petals pale green in vivo, elliptic, 20–25 by 7–11 mm, outer side densely to finally sparsely covered with erect, more or less curly hairs; stamens 1.5–2 mm long, connective shield papillate, flat to umbonate. *Monocarps* 8–10, black in vivo, brown in sicco, ellipsoid, 8–11 by 7–8 mm, glabrous, apex apiculate (apiculum < 0.5 mm long), wall c. 0.1 mm thick, stipes 17–20 by c. 1 mm. *Seed* ellipsoid, c. 10 by 6 mm, dark, shiny brown, pitted, raphe slightly raised.

Distribution — Guyana (Merume Mts).

Habitat & Ecology — In forest, along ridge trail of mountain. At an elevation of c. 500 m. Flowering: July; fruiting: July.

Vernacular names — Not recorded.

Note — *Guatteria partangensis*, only known from the type collection, slightly resembles *G. ouregou*, a species restricted to French Guiana, due to its erect, long hairs on young twigs and pedicels. It differs from the latter by a lower number of secondary veins (6–9 vs 11–15) and longer pedicels (40–50 vs 10–25 mm).

121. *Guatteria pastazae* R.E.Fr. — Map 26

Guatteria pastazae R.E.Fr. (1947) 5, t. 2; Erkens et al. (2008) 505, f. 16, pl. 1; Maas & Westra (2011) 137. — Type: *Lugo 181* (holo S; iso G, US), Ecuador, Pastaza, Mera, c. 600 m, 4 Apr. 1940.

Tree 4–30 m tall, 8–60 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 oblong-elliptic 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 or rarely not 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, sparsely covered with appressed hairs below, base attenuate, basal margins often revolute, apex acuminate (acumen 10–15 mm long), primary vein impressed to flat above, slightly keeled below, secondary veins indistinct, 12–17 on either side of primary vein, slightly raised above, smallest distance between loops and margin 1–5 mm, tertiary veins flat to slightly raised above, reticulate. *Flowers* in 1(–3)-flowered inflorescences in axils of leaves or sometimes on leafless branchlets; pedicels 3–15 mm long, 1–2.5 mm diam, fruiting pedicels to c. 25 mm long, to c. 3 mm diam, densely to rather densely covered with appressed, brown hairs, articulated at 0.2–0.7 from the base, bracts 5–7, soon falling and leaving prominent scars, uppermost bracts elliptic, 6–12 by 3–6 mm; flower buds ovoid to broadly ovoid; sepals basally connate or free, broadly to shallowly ovate-triangular, 4–10 by 5–8 mm, appressed, but soon becoming spreading to finally reflexed, outer side densely covered with appressed, brown hairs; petals green or greenish yellow and slightly tinged with red in vivo, elliptic-oblong to elliptic-obovate, 12–20{–28} by 6–12 mm, outer side densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate to 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, soon 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, transversely grooved to pitted, raphe raised.

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

Habitat & Ecology — In premontane or montane forest, rarely in lowland rain forest, on soils derived from sandstone substrate or on red clay. At elevations of 0–2550 m. Flowering: November to May, August; fruiting: June to March.

Vernacular names — Peru: Palo yais (Shuar name) (*Ancuash 469*), Wampu yais (Shuar name) (*Ancuash 469*, *Kayap 801*), Yais (Shuar name) (*Kajekai & Wisum 483*, *Rojas et al. 150*, *Wisum & Kajekai 726*).

Additional specimens 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 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* but it differs by its much shorter stipes (stipes shorter than to almost equalling monocarp length vs stipes longer than the monocarp in *G. modesta*).

After the publication of Erkens' et al. (2008), the present authors investigated a specimen far removed from Ecuador and Peru, namely *Sothers et al. 540* from the lowlands of Amazonian Brazil, near Manaus. As that collection nicely matched with *G. pastazae* in all essential features (inconspicuous leaf venation, wrinkled fruits, etc.), we included it, thereby extending the known range of *G. pastazae* to the east.

122. *Guatteria peruviana* R.E.Fr. — Map 26

Guatteria peruviana R.E.Fr. (1938) 720; Maas & Westra (2011) 139, f. 19, 20. — Type: *Killip & Smith 27522* (holo F; iso B, NY, US 2 sheets), Peru, Loreto, Rio Marañon, near mouth of Río Tigre, 115 m, 19 Aug. 1929.
Guatteria macrocarpa R.E.Fr. (1938) 719; (1939) 492, f. 27a, b. — Type: *Killip & Smith 28965* (holo F; iso B, NY, US), 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, tertiary veins slightly raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 7–12 mm long, 1–1.5 mm diam, fruiting pedicels to c. 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, not seen; 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 in vivo, narrowly 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, colour in vivo not recorded, 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, rugose, longitudinally and transversely grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Peru (Loreto).

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

Vernacular names — Not recorded.

Note — *Guatteria peruviana* is recognizable by a combination of verruculose leaves and short pedicels and stipes. Moreover, the seeds are quite remarkable by an impressed raphe and the presence of longitudinal and transversal grooves.

123. *Guatteria pichinchae* Maas & Westra, *sp. nov.* — Fig. 58; Plate 6f; Map 27

Probabiliter *G. goudotianae* proxima sed ab a differt venis secundariis impressis pedicellis longioribus et monocarpiis minoribus. — Typus: *Cornejo & Montenegro 8355* (holo NY; iso U), Ecuador, Pichincha, Ayapi Pachijal, 1220 m, 18 Nov. 2010.

Tree 7–20 m tall, 7–8 cm diam; young twigs densely to sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 7–17 mm long, 2–2.5 mm diam; lamina elliptic, ovate, obovate or narrowly so, 10–24 by 4–9 cm (leaf index 2.1–3.1), coriaceous, not verruculose, dull, rarely shiny, greyish green above, greyish green to greenish brown below, glabrous above, sparsely densely covered with appressed hairs to glabrous below, base acute to obtuse, sometimes attenuate, apex acuminate (acumen 5–15 mm long) to acute, primary vein impressed above, secondary veins distinct, 12–20 on either side of primary vein, impressed above, smallest distance between loops and margin 3–8 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 25–80 mm long, 1–1.5 mm diam, fruiting pedicels to 1.5 mm diam, sparsely to densely covered with appressed hairs, articulated at 0.1–0.3 from the base, bracts 5–6, not seen except for incidental foliaceous upper bracts, these narrowly elliptic to elliptic, 12–27 by 4–12 mm; flower buds not seen; sepals free, broadly ovate-triangular, 3–5 by 3–5 mm, appressed, but apex and margins often reflexed, outer side rather densely covered with appressed hairs; petals green to yellow in vivo, elliptic-ovate to narrowly so, 10–20 by 4–11 mm, outer side densely covered with erect to appressed, curly hairs; stamens 2–2.5 mm long, connective shield papillate. *Monocarps* 10–50, green to purple in vivo, black in sicco, ellipsoid, 10–12 by 4–7 mm, glabrous or sparsely covered with appressed hairs, apex apiculate (apiculum < 1 mm long) or rounded, wall 0.5–1{–1.5} mm thick, stipes 5–12 by 1 mm. *Seed* ellipsoid, 9–10 by 4–5 mm, brown, pitted to transversely grooved, raphe raised.

Distribution — Ecuador (Esmeraldas, Pichincha).

Habitat & Ecology — In lowland or montane forest or roadside margin. At elevations of 0–1460 m. Flowering: March, April, August, October, November; fruiting: March, July, October, November.

Vernacular names — Not recorded.

Other specimens examined. Ecuador, **Esmeraldas**, Eloy Alfaro Canton, along road between Esmeraldas and Borbón, between Lagarto and Borbón, 2.5 km W of Borbón, 50 m, *Croat 73107* (L, MO); Borbón, sea level, *Little 6367* (K). **Pichincha**, road from Quito to La Concordia via Nono, Mindo, San José de las Minas and Puerto Quito, 1460 m, *Dodson et al. 15203* (U); Finlandia, 16 km E of Santo Domingo de los Colorados, 680 m, *Gentry et al. 12146* (MO, NY, U); road Pacto-Nuevo Azuay, 10 km N of La Esperanza, 1150 m, *Holm-Nielsen et al. 24566* (AAU, U).

Note — *Guatteria pichinchae* probably comes closest to *G. goudotiana*, sharing coriaceous leaves and long pedicels. It differs by its impressed secondary veins (vs slightly raised in *G. goudotiana*), much longer pedicels (25–80 vs 10–30 mm long) and by smaller monocarps (< 12 mm vs to 20 mm long). Flower colour is reported in *G. pichinchae* to vary from green to yellow, whereas *G. goudotiana* is reported to have greyish to black petals.

124. *Guatteria pittieri* R.E.Fr. — Fig. 59; Map 26

Guatteria pittieri R.E.Fr. (1939) 516. — Type: *Pittier 531* (holo US 2 sheets), Colombia, Valle del Cauca, Córdoba, Dagua Valley, Pacific Coastal Zone, 30–100 m, Dec. 1905.
Guatteria sphaerantha R.E.Fr. (1950a) 334, pl. 1, syn. nov — Type: *Cuatrecasas 17579* (holo S; iso COL 2 sheets, F 2 sheets, S, US 2 sheets), Colombia, Valle del Cauca, Costa del Pacífico, Río Cajambre, Silva, 5–80 m, 5 May 1944.
Guatteria columbiana R.E.Fr. (1950a) 335, pl. 2, syn. nov. — Type: *Cuatrecasas 21274* (holo S 2 sheets; iso COL 2 sheets, F, S, US 2 sheets), Colombia, Valle del Cauca, Río Calima (Chocó region), Quebrada de La Brea, 20–40 m, 24 May 1946.

Tree or rarely a shrub 3–22 m tall, 3–40 cm diam; young twigs rather densely to sparsely covered with appressed, white hairs, soon glabrous. *Leaves*: petiole 4–20 mm long, 1–3 mm diam, often winged; lamina narrowly elliptic to narrowly obovate, 13–36 by 4–12 cm (leaf index 2.6–5), chartaceous, sparsely verruculose above at the base and along the margin of the veins or not verruculose, dull, dark brown to greenish above, duller and paler brown to greenish below, sparsely covered with appressed, white hairs to glabrous above, rather densely to sparsely covered with appressed, white hairs to glabrous below, base long-attenuate, apex acuminate (acumen 5–15 mm long), rarely acute, primary vein impressed above, often keeled below, secondary veins distinct, 12–20 on either side of primary vein, raised above, smallest distance between loops and margin 1–5 mm, tertiary veins slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 25–60 mm long, 1–2 mm diam, fruiting pedicels to c. 3 mm diam, rather densely to sparsely covered with appressed, brown hairs, articulated at 0.2–0.3 from the base, bracts 3–7, soon falling, elliptic, the basal ones to c. 1 mm long, the 2 upper ones 4–6 mm

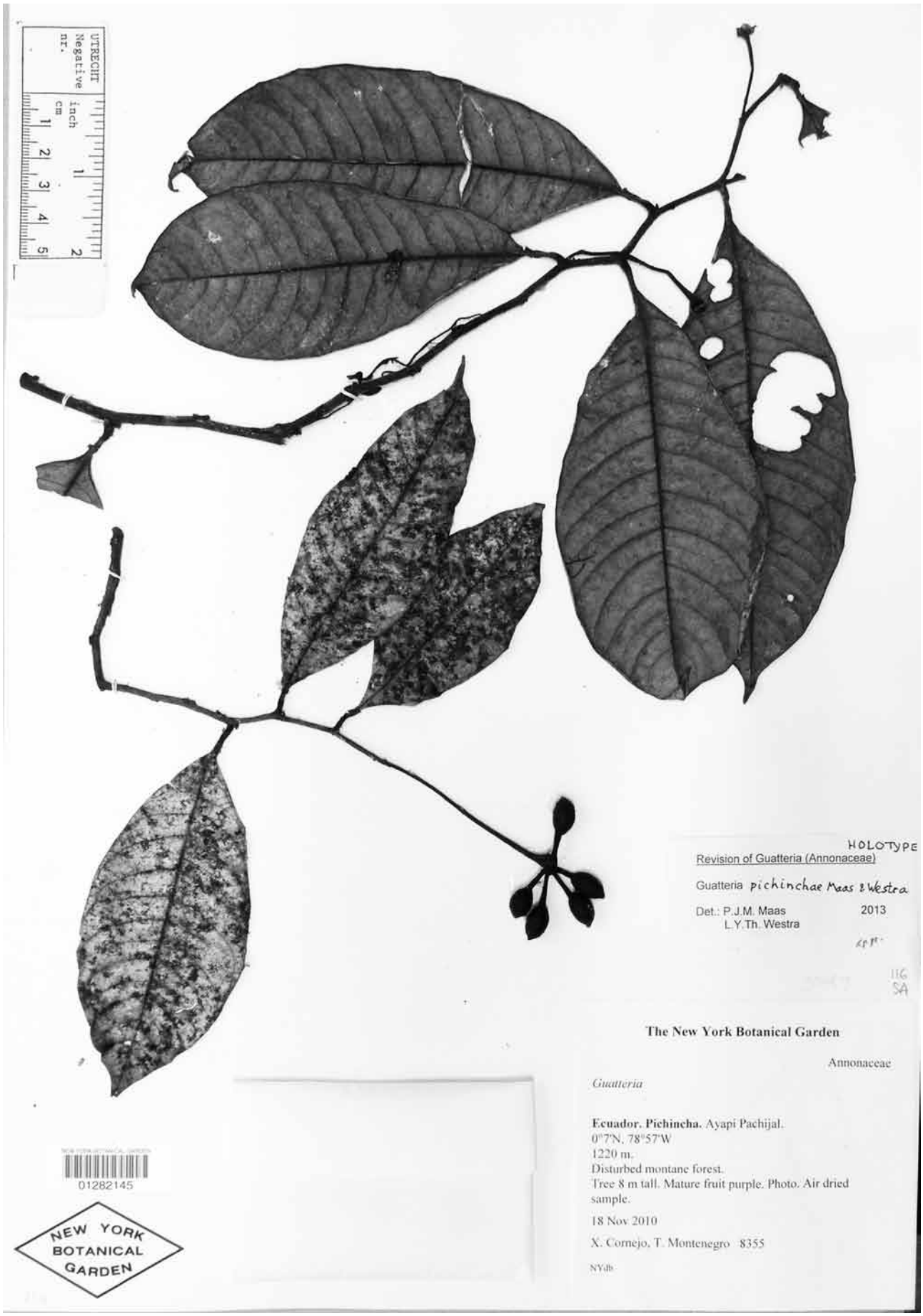


Fig. 58 *Guatteria pichinchae* Maas & Westra. Fruiting branch (*Cornejo & Montenegro 8355*, holotype NY).

long; flower buds ovoid to depressed ovoid; sepals free, broadly ovate-triangular to shallowly ovate-triangular, 3–10 by 4–8 mm, appressed, outer side rather densely covered with appressed, brown hairs; petals green, yellowish green or cream in vivo, elliptic to ovate to broadly so, 9–30 by 8–20 mm, outer side densely to rather densely covered with appressed, brown hairs; stamens 2–2.5 mm long, connective shield papillate. *Monocarps* 15–60, green, maturing purple-black to black in vivo, dark brown in sicco, ellipsoid to obovoid, 8–14{–15} by 3–7{–10} mm, sparsely covered with appressed, brown hairs, apex apiculate (apiculum c. 0.5 mm long), wall 0.1–0.3 mm thick, stipes 6–20 by 0.5–1.5 mm. *Seed* ellipsoid, 7–14 by 3–6 mm, dull, reddish brown to brown, rugose, raphe raised.

Distribution — Colombia (Antioquia, Chocó, Nariño, Valle del Cauca), Western Ecuador (Carchi, Esmeraldas, Pichincha).

Habitat & Ecology — In montane, premontane or lowland (sometimes disturbed) forest, along margins of creeks or rivers, slopes and roadsides, on reddish yellow or yellowish grey, clayey loam. At elevations of 0–1900 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Colombia: Cargadero (*Monsalve B.556*), Cargadero blanco (*D.A. Sánchez S. et al. 883*, *884A*). Ecuador:

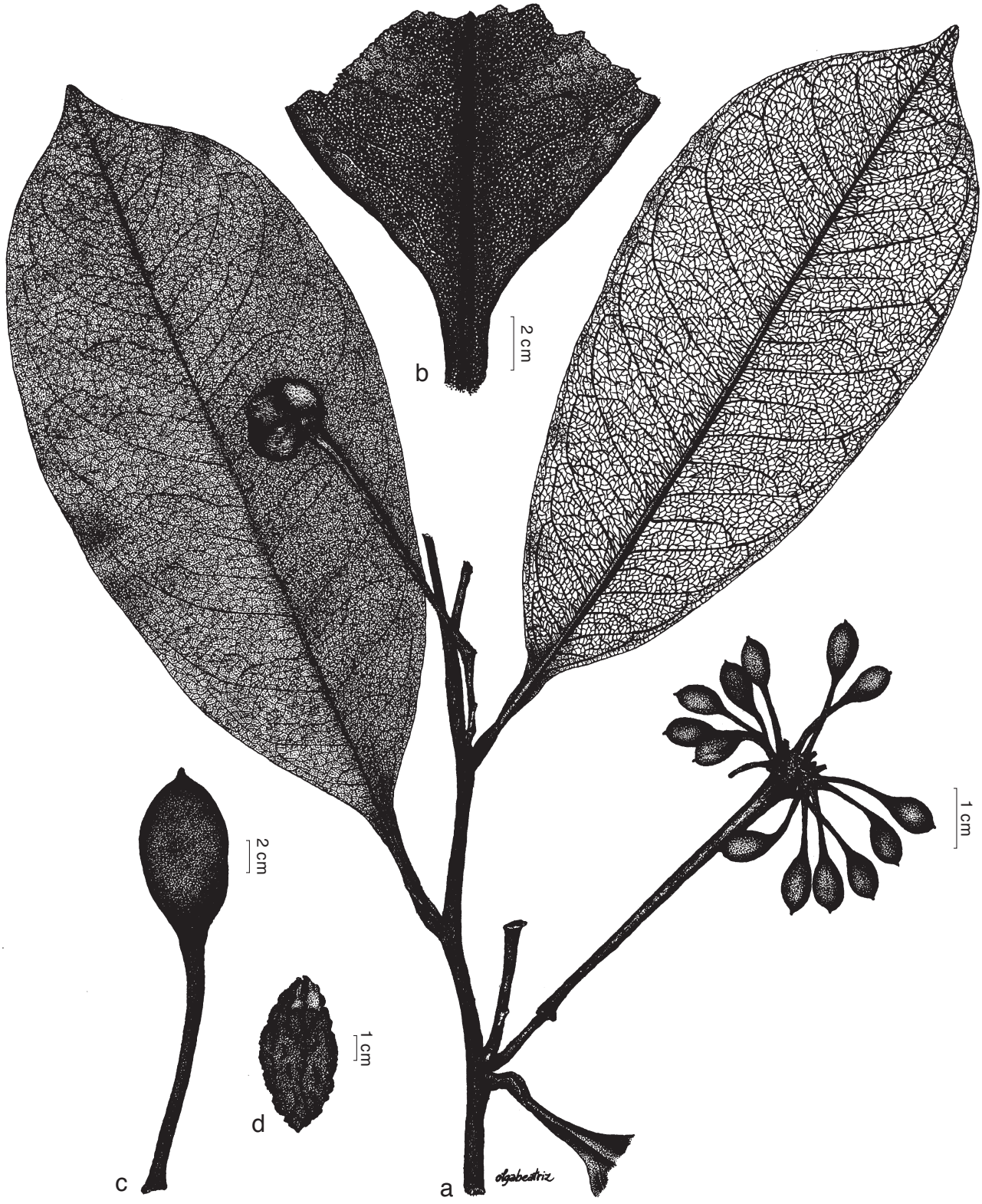


Fig. 59 *Guatteria pittieri* R.E.Fr. a. Flowering branch; b. lower side of lamina; c. monocarp; d. seed (all: *D.A. Sánchez S. & Hoyos M. 721*, MEDEL; from Sánchez S. (1986) f. 25).

Cargadera negra (*Grijalva et al. 471*, *Méndez et al. 257*, *Quelal et al. 599*, *603*), Guasca negra (*Quelal et al. 691*, *Tipaz et al. 1062*), Ñinchu (*Tipaz et al. 2488*), Tetalde (Awaví name) (*Grijalva et al. 471*).

Uses — Ecuador: Bark used for making baskets (*Quelal et al. 599*, *603*).

Notes — *Guatteria pittieri* can be recognized by narrowly elliptic to narrowly obovate leaves with long petioles and a long-attenuate leaf base. Further characteristics are the relatively long and slender pedicels up to 60 mm long.

Guatteria columbiana, *G. sphaerantha* and *G. pittieri* were treated by Sánchez S. (1987) as different species. He distinguished between them depending on the density of verruculae and where they could be found. Verruculae are not always a constant character that can be found on the leaves in the different specimens that we have examined, making this character unreliable for separating species.

Guatteria sphaerantha, now a synonym of *G. pittieri*, was wrongly treated by Murillo A. & Restrepo (2000). They described it as a cauliflorous species, a character that is absent in *G. pittieri*, and, in addition, is rare in the whole genus. The specimens: *Murillo A. & Román 605* (COAH, COL, U), *Murillo A. et al. 884* (COAH, COL, U) and *Gentry & D A. Sánchez S. 64984* (COAH, MO, U) belong to *G. scalarinervia*. These three collections are the first gatherings of this species from Caquetá, in the Colombian Amazon region. Formerly, *G. scalarinervia* was known from Ecuador and Peru only.

Boyle et al. 1525, *1780*, *2144* (U), *Palacios & Tirado 4375* (U) and *Tipaz et al. 1841* (U) from Ecuador are aberrant by having erect hairs on the leafy twigs and lower side of the leaves, but otherwise they match this species very well

125. *Guatteria pogonopus* Mart. — Fig. 60; Map 26

Guatteria pogonopus Mart. (1841) 34; R.E.Fr. (1939) 402. — Type: *Sellow s.n.* (lecto B, selected by Fries 1939; isolecto K), Brazil, Bahia, Nazaré das Farinhas ('Nazareth'), 1817.

Guatteria schlechtendaliana Mart. (1841) 34; R.E.Fr. (1939) 406, t. 26. — Type: *Martius s.n.* (holo BR 3 sheets), Brazil, Bahia, Ilhéus, Fazenda Almada.

Tree or shrub 2–15 m tall, 5–15 cm diam; young twigs densely to sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 4–12 mm long, 2–5 mm diam; lamina narrowly elliptic to elliptic, 13–35 by 4–13 cm (leaf index 1.9–2.7), chartaceous to subcoriaceous, not verruculose, brown above, pale brown below, glabrous on both sides, base obtuse, apex acute, primary vein impressed above, secondary veins indistinct, 13–18 on either side of primary vein, raised above, smallest distance between loops and margin c. 2 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 5–15 mm long, c. 2 mm diam, fruiting pedicels 15–30 mm long, 3–4 mm diam, densely covered with appressed, brown hairs to glabrous, articulated at 0.2–0.3 from the base, bracts 2, soon falling, 2–5 mm long; flower buds broadly ovoid; sepals free, broadly ovate-triangular, 4–6(–12) by 4–7(–12) mm, reflexed, outer side glabrous or sometimes densely covered with appressed hairs; petals cream or yellow in vivo, elliptic to narrowly elliptic, 7–25 by 4–12 mm, outer side sparsely covered with curly, brown hairs to glabrous; stamens

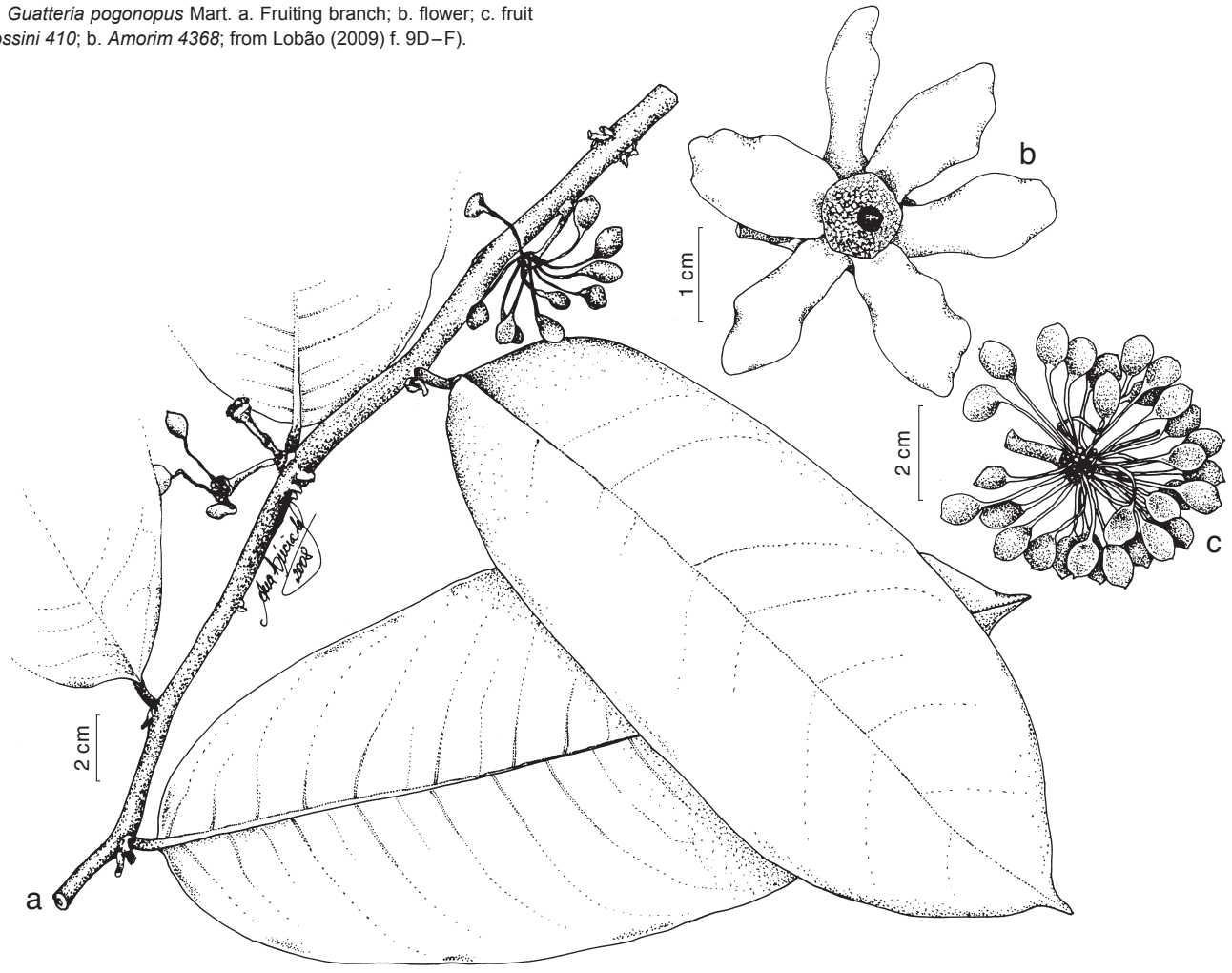


Fig. 60 *Guatteria pogonopus* Mart. a. Fruiting branch; b. flower; c. fruit (a, c. *Rossini 410*; b. *Amorim 4368*; from Lobão (2009) f. 9D–F).

c. 1.5 mm long, connective shield hairy. *Monocarps* 15–40, green, maturing purple-black to black in vivo, black in sicco, ellipsoid, 10–12 by 5–7 mm, glabrous, apex apiculate (apiculum c. 0.3 mm long), wall 0.5–1 mm thick, stipes 10–17 by 1 mm. *Seed* ellipsoid, 10–12 by 5–7 mm, pale to dark brown, smooth to pitted, raphe raised.

Distribution — Brazil (Alagoas, Bahia, Ceará, Espírito Santo, Mato Grosso, Minas Gerais, Paraíba, Pernambuco).

Habitat & Ecology — In non-inundated, Atlantic rain forest, on clayey soil. At elevations of 0–1050 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Not recorded.

Note — *Guatteria pogonopus* is easily recognized by its large and glabrous leaves, and rather shortly pedicellate flowers and fruit. It is similar to *G. oligocarpa* and *G. ferruginea* (see comments with the respective species).

126. *Guatteria pohliana* Schltdl. — Fig. 61; Map 27

Guatteria pohliana Schltdl. (1834) 321; R.E.Fr. (1939) 332, f. 5a, b. — Type: *Sellow 1132* (holo BR; iso B, K, P), Brazil, Minas Gerais, without location.

Tree or shrub 1.5–10 m tall, 6–20 cm diam; young twigs densely covered with appressed hairs to glabrous. *Leaves*: petiole 2–5 mm long, c. 1 mm diam; lamina narrowly elliptic to elliptic, 4–12 by 1.5–3.5 cm (leaf index 2.3–4.5), chartaceous, not verruculose, dull, dark brown above, pale brown below, sparsely covered with appressed hairs to glabrous above and below, base acute, apex acute, primary vein slightly impressed above, secondary veins indistinct, 7–12 on either side of primary vein, raised above, smallest distance between loops and margin 1–3 mm, tertiary veins inconspicuous, raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 10–30 mm long, 0.5–1 mm diam, fruiting pedicels to c. 35 mm long, to 1.5 mm diam, sparsely covered with appressed, brown hairs, articulated at c. 0.2 from the base, bracts 1–2, soon falling, 7–20 by 4–10 mm; flower buds broadly ovoid; sepals free or initially connate, broadly ovate-triangular, 5–7 by 5–7 mm, reflexed, outer side glabrous; petals pale yellow in vivo, ovate, 6–20 by 4–7 mm, outer side sparsely covered with erect, curly pale brown hairs; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* 20–30, green, maturing purple-black in vivo, black in sicco, ellipsoid, 8–10 by 5–7 mm, sparsely covered with erect, pale brown hairs, soon glabrous, apex apiculate (apiculum c. 0.5 mm long), wall 0.2–0.5 mm thick, stipes 5–9 by 1 mm. *Seed* ellipsoid, 8–10 by 5–7 mm, brownish red, pitted to transversely grooved, raphe raised.

Distribution — Brazil (Bahia, Espírito Santo, Minas Gerais).

Habitat & Ecology — In non-inundated forest, often on clayey soil. At elevations of 0–1280 m. Flowering: March to May, September; fruiting: January to March, August to December.

Vernacular names — Brazil: Araticum (*Forzza 4427*), Imbiú-pimenta (*Guedes RB 290854*).

Note — *Guatteria pohliana* is characterized by small leaves, mostly not exceeding 10 cm in length, often glabrous on both sides. According to Lobão & Mello-Silva (2007) the floral buds are black, glabrous, with the sepals fully connate, all of which are also noteworthy features; the latter feature should serve to distinguish *G. pohliana* from small-leaved specimens of *G. australis* where the sepals are free in bud. In practice this will probably be difficult to verify. Fries (1939) also mentions the small and sparsely hairy petals, the variable length of the fruiting pedicel, and the large monocarps. It should be added, too, that *G. australis* generally has longer pedicels than *G. pohliana*. Similarly, *G. pohliana* may resemble small-leaved specimens of the equally small-leaved *G. sellowiana*, but the latter is immediately distinct by branches, leaves and floral pedicels being densely covered with hairs.

127. *Guatteria polyantha* R.E.Fr. — Map 27

Guatteria polyantha R.E.Fr. (1939) 475, f. 24f, g. — Type: *Monteiro da Costa 284* (holo S; iso F 2 sheets), Brazil, Pará, Tapajós, Cajatuba, 20 Jan. 1932.

Tree 18 m tall, c. 44 cm diam; young twigs rather densely covered with erect, brown hairs, soon glabrous. *Leaves*: petiole 3–4 mm long, 1–2 mm diam; lamina narrowly elliptic, 6–10 by 2–3 cm (leaf index 3–4), chartaceous, not verruculose, dull, greyish above, greyish brown below, sparsely covered with erect hairs above, soon glabrous, sparsely covered with erect hairs below, the primary vein sparsely to rather densely covered with erect hairs, base acute to obtuse, apex acuminate (acumen to c. 5 mm long), primary vein impressed above, secondary veins distinct, 12–14 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences, in axils of leaves or on leafless branchlets; pedicels 10–15 mm long, 1–2 mm diam, rather densely to sparsely covered with erect hairs, articulated at c. 0.4–0.7 from the base, bracts 5–7, soon falling, not seen; flower buds depressed ovoid, obtuse; sepals free, broadly ovate-triangular, c. 4 by 4 mm, appressed, at last reflexed, outer side rather densely to sparsely covered with appressed hairs; petals colour in vivo not recorded, narrowly obovate, 10–15 by 7–10 mm, outer side densely covered with appressed, brown hairs; stamens c. 1 mm long, connective shield densely hairy. *Monocarps* and *seed* not seen.

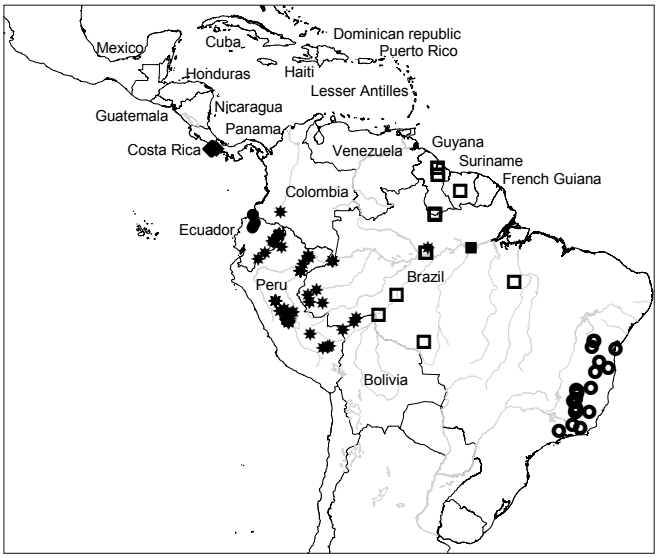
Distribution — Brazil (Pará).

Habitat & Ecology — In 'highland'. At low elevations. Flowering: January; fruiting: not recorded.

Vernacular name — Brazil: Envira-amarela ('amarella').

Uses — Brazil: 'Wood for civil constructions and furniture' (*Monteira da Costa 284*).

Note — *Guatteria polyantha* is only known from the type collection. It was placed by Fries (1939) in sect. *Trichostemon* with *G. foliosa*, *G. maypurensis* and *G. trichostemon*, all characterized by hairy connective shields and small leaves. A noteworthy feature is the location of the articulation of the pedicel, usually above the middle. Its systematic position is still unclear.



Map 27 Distribution of *Guatteria pinchinchae* (●), *G. pohliana* (✪), *G. polyantha* (■), *G. procera* (□), *G. pudica* (◆) and *G. ramiflora* (✱).

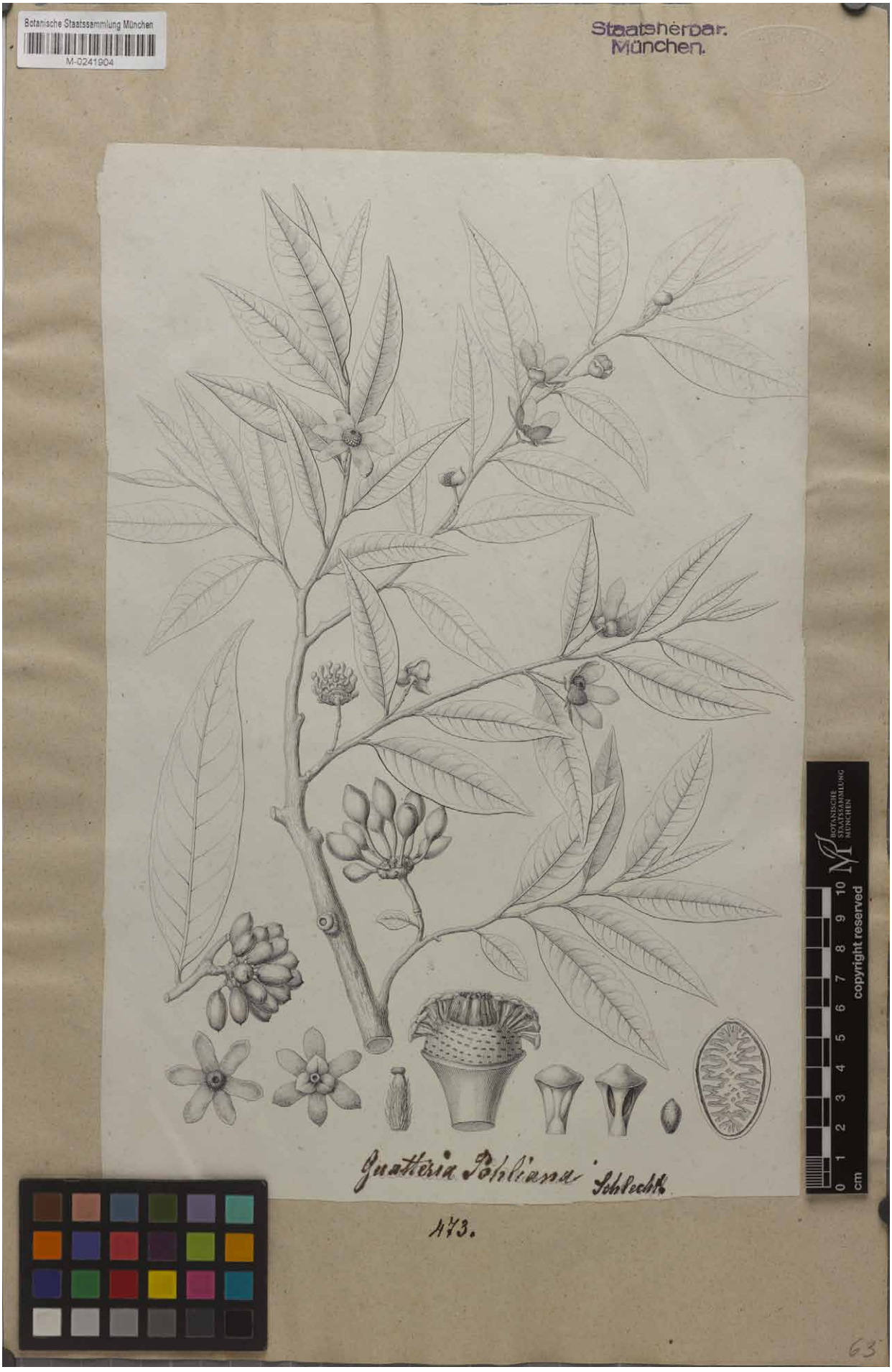


Fig. 61 *Guatteria pohliana* Schltdl. Flowering and fruiting branch; left: fruit and leaf; bottom from left to right: flower from above, flower from below, a carpel (pistil), floral receptacle with (part of) stamens and pistils left in place, a stamen before and after dehiscence, a seed, and seed in longitudinal section. – Used as illustration in Martius, Flora Brasiliensis 13, 1 (1841) t. 9, f. 2. With kind permission of Botanische Staatssammlung München.

Fig. 62 *Guatteria procera* R.E.Fr. Flowering branch (*Teixeira et al. 906*, U).

128. *Guatteria procera* R.E.Fr. — Fig. 54e, 62; Map 27

Guatteria procera R.E.Fr. (1948a) 230. — Type: *Forest Department British Guiana 3676 = Fanshawe 940* (holo K 2 sheets; iso FDG, K 2 sheets, NY, P, S, U), Guyana, Lower Essequibo River, Barbara Creek, 26 Nov. 1942.

Guatteria brachypoda R.E.Fr. (1948a) 231. — Type: *Forest Department British Guiana 3474 = Fanshawe 738* (holo K 3 sheets; iso FDG, NY, S, U), Guyana, Mazaruni Station, 23 June 1942.

Guatteria williamsii R.E.Fr. (1950a) 332. — Type: *Ll. Williams 15559* (holo S; iso F, G, NY, RB, US 2 sheets, VEN), Venezuela, Amazonas, Upper Río Casiquiare, Capibara ('Capihuara'), 120 m, 26 May 1942.

Tree 3–27 m tall, 4–90 cm diam; young twigs densely covered with erect, brown hairs, eventually glabrous. *Leaves*: petiole 4–11 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly ovate, 8–17 by 3–6 cm (leaf index 2.3–3.9), chartaceous, not verruculose, shiny and dark brown above, paler brown below, sparsely covered with erect hairs above, but primary vein mostly densely covered with erect hairs, densely to sparsely covered with erect (rarely appressed in part) hairs below, base attenuate to obtuse, apex acute to acuminate (acumen 5–25 mm long), primary vein slightly raised or flat above, secondary veins distinct, 10–15 on either side of primary vein, slightly raised to flat above, smallest distance between loops and margin 2–5 mm, tertiary veins slightly raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves, rarely on leafless branchlets; pedicels 12–25 mm long, 1–1.5 mm diam, fruiting pedicels to c. 2 mm diam, densely covered with appressed to erect hairs, articulated at 0.2–0.5 from the base, bracts c. 5, soon falling, broadly ovate to broadly elliptic, basal bracts c. 1.5 mm long, uppermost bracts to c. 6 mm long; flower buds broadly ovoid to broadly ellipsoid; sepals free or basally connate, broadly ovate-triangular, 4–6 by 3–7 mm, reflexed, outer side densely covered with appressed, pale brown hairs; petals green, yellow, or cream in vivo, narrowly obovate to obovate, 15–21 by 5–10 mm, outer side densely to sparsely covered with appressed hairs; stamens 1–1.5 mm long, connective shield papillate, flat or slightly umbonate. *Monocarps* 20–50, maturing black in vivo, brown to black in sicco, ellipsoid, 8–12 by 4–6 mm, sparsely covered with appressed hairs, apex apiculate (apiculum 0.2–0.5 mm long), wall 0.1–0.2 mm thick, stipes (10–)15–25 by 0.5–1 mm. *Seed* narrowly ellipsoid to narrowly ovoid, 8–11 by 3–5 mm, pale to dark brown, pitted to transversely grooved, raphe impressed.

Distribution — Amazonian Venezuela (Amazonas), Guyana, Suriname, Amazonian Brazil (Amazonas, Pará, Rondônia).

Habitat & Ecology — In non-inundated, primary or secondary forest, or savanna, 'on peat and granite, or on granite boulders'. At elevations of 100–1100 m. Flowering: March, June, August, September, November; fruiting: June, August, September.

Vernacular names — Guyana: Smooth skin arara (Arawak name) (*Forest Department British Guiana 3474 = Fanshawe 738*, *Forest Department British Guiana 3676 = Fanshawe 940*). Suriname: Boszuurzak (Surinamese name). Venezuela: Majagua (*Ll. Williams 15559*).

Note — *Guatteria procera* and *G. monticola*, published a few years later by Fries (1952a), look very similar, but are distinct in a number of features. In *G. procera*, most notably, the primary vein is flat or even slightly raised above, while in *G. monticola* the primary vein is impressed. The hairs on the lower side of the leaves of *G. procera* are erect (or rarely appressed on part of the lower surface only), while these hairs are clearly appressed in *G. monticola*. Further differences, though less conspicuous, may be noted as well: *G. procera* – young twigs with erect hairs, leaf base varying from attenuate to obtuse, smallest distance between loops of secondary veins and leaf margin 2–5 mm; *G. monticola* – young twigs with appressed to erect hairs, leaf base acute, smallest distance between loops of secondary veins and margin 1–2 mm.

129. *Guatteria pudica* N.Zamora & Maas — Map 27

Guatteria pudica N.Zamora & Maas (2000) 244, f. 3–5. — Type: *Herrera C. 4026* (holo INB; iso BM, CR, MO), Costa Rica, Puntarenas, Peninsula de Osa, Parque Nacional Corcovado, Rincón, 'por las filas en la cuenca superior de la Quebrada Vaquedano', 500 m, 23 July 1990.

Tree 4–13 m tall, 5–40 cm diam; young twigs densely covered with a long-persisting indument of erect, reddish brown hairs. *Leaves*: petiole 3–8 mm long, 2–3 mm diam; lamina narrowly elliptic to narrowly oblong-elliptic, 10–28 by 5–10 cm (leaf index 2–3), chartaceous, not verruculose, dull, greyish green above, brown below, glabrous above, but primary vein densely covered with erect, reddish brown hairs, densely covered with erect, reddish brown hairs below, base obtuse to slightly cordate, basal margins revolute or slightly so, apex acuminate (acumen 10–20 mm long), primary vein impressed to flat above, secondary veins distinct, 7–16 on either side of primary vein, impressed to slightly raised above, smallest distance between loops and margin 3–5 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 10–17 mm long, 2–3 mm diam, fruiting pedicels to c. 35 mm long, 2–3 mm diam, densely covered with erect and appressed, reddish brown hairs, articulated at 0.2–0.6 from the base, bracts 4–7, soon falling, lower bracts broadly to very broadly elliptic-ovate, c. 2 mm long, uppermost bracts broadly elliptic, 4–6 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 5–8 by 5–8 mm, appressed to slightly reflexed, outer side densely covered with appressed hairs; petals yellowish green or yellow in vivo, broadly ovate to rhombic, 10–20 by 9–18 mm, outer side densely covered with appressed, reddish brown hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 50–75, wine-red when ripe in vivo, black in sicco, ellipsoid, 8–11{–13} by 4–6{–8} mm, sparsely covered with appressed hairs, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 5–10 by 1 mm. *Seed* ellipsoid, 7–8 by 4 mm, dark brown, pitted, raphe not distinct from rest of seed.

Distribution — Costa Rica.

Habitat & Ecology — In lowland rain forest. At elevations of 0–500(–800) m. Flowering: February, March, May, July, November; fruiting: February, May, June, November.

Vernacular name — Costa Rica: Malagueto (*Thomson 742*).

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

130. *Guatteria punctata* (Aubl.) R.A.Howard — Fig. 63; Map 28

Guatteria punctata (Aubl.) R.A.Howard (1983) 260. — *Annona punctata* Aubl. (1775) 614, t. 247. — Type: *Aublet s.n.* (lecto BM, selected by Howard 1983), French Guiana, Sinnamary ('Habitat in sylvis Sinemariensibus & prope amnem Galibiensem').

Guatteria glauca Ruiz & Pav. (1798) 145; R.E.Fr. (1939) 384, f. 13a, b; Maas & Westra (2010) 267, pl. 1, syn. nov. — Type: *Ruiz L. s.n.* (syn B, BR, F, G, HAL, K, MA, NY, P), Peru, Huánuco, 'Habitat in Peruviae in nemoribus versus Cochero et Chinchao vicos', anno 1798.

Annona axilliflora DC. (1824) 86. — *Guatteria axilliflora* (DC.) R.E.Fr. (1939) 427, f. 15a. — Type: *Martin 151* (holo G; iso C, K 2 sheets, P 4 sheets), French Guiana ('Cayenne'), without location.

Guatteria caniflora Mart. [var. *caniflora*] Mart. (1841) 37, syn. nov. — *Guatteria caniflora* Mart. var. *angustifolia* Mart. (1841) 37; R.E.Fr. (1939) 442. — Type: *Martius s.n.* (holo M), Brazil, Amazonas, Rio Solimões ('prov. Rio Negro, in sylvis inundatis ad fluv. Solimões'), Nov.–Dec. 1819.

Guatteria caniflora Mart. var. *latifolia* Mart. (1841) 37; R.E.Fr. (1939) 442, syn. nov. — Type: *Martius s.n.* (holo M, not seen), Brazil, Amazonas, Rio Solimões, Dec. 1819 ('prov. Rio Negro, in sylvis ad fluvium Solimões').

Guatteria poeppigiana Mart. (1841) 37 (as '*pöppigiana*'); R.E.Fr. (1939) 424, syn. nov. — Type: *Poeppig D2963* (lecto W, selected by Fries 1939, not seen), Brazil, Pará, Colares ('in silvis ad collares'), June 1838.

Annona chrysopetala Steud. (1843) 754. — *Guatteria chrysopetala* (Steud.) Miq. var. *chrysopetala* (1849) 466; R.E.Fr. (1939) 434. — Type: *Hostmann & Kappler 1295*, *ed. Hohenacker* = *Hostmann 1295* (holo P; iso B, BM, G 3 sheets, GH, K, MO, P, S, U, UPS, W), Suriname, Suriname River.

Guatteria pteropus Benth. (1853) 8, syn. nov. — Type: *Spruce 1680* (holo K; iso BM, E, G 3 sheets, K, M, NY, P), Brazil, Amazonas, mouth of Rio Negro, Aug. 1851.

Guatteria cargadero Triana & Planch. (1862) 34; R.E.Fr. (1939) 380, syn. nov. — Type: *Triana s.n.* (holo P; iso B, BM, BR, G, W), Colombia, Valle del Cauca, Anserma, 1000 m.

Guatteria platyphylla Triana & Planch. (1862) 35; R.E.Fr. (1939) 449, syn. nov. — Type: *Triana s.n.* (holo P; iso BM, COL), Colombia, Cundinamarca, Servita, 1000 m, ('Servita, versant oriental des Andes de Bogota, alt. 800 mêtres').

Guatteria sylvicola S.Moore (1895) 298, syn. nov. — Type: *Spencer Moore 142* (holo BM; iso B), Brazil, Mato Grosso, Serra da Chapada, 600 m, Aug. 1891.

Guatteria coeloneura Diels (1906) 408; R.E.Fr. (1939) 387, f. 13c, syn. nov. — Type: *Weberbauer 3548* (holo B 3 sheets; iso F, G, S), Peru, Huánuco, SW of Monzón, 1600 m, 8 Aug. 1903.

Guatteria pleiocarpa Diels (1906) 409; R.E.Fr. (1939) 387, f. 12e, syn. nov. — Type: *Weberbauer 4530* (holo B 3 sheets; iso F, G 4 sheets, GH), Peru, Loreto, Moyobamba, 800–900 m, 17 Aug. 1904.

Guatteria guentheri Diels (1927) 169; R.E.Fr. (1939) 433, f. 14b, c, syn. nov. — Type: *Tessmann 4387* (holo B 2 sheets; F fragment, NY, S fragment), Peru, Loreto, Upper Río Marañon, near mouth of Río Santiago, 160 m, 27 Oct. 1924.

Guatteria atra Sandwith (1930) 468, syn. nov. — Type: *Sandwith 406* (holo K; iso B, FDG, K 2 sheets, NY, P, RB, U, US), Guyana, Moraballi Creek, Essequibo River, 9 Oct. 1929.

Guatteria acutissima R.E.Fr. (1938) 712; (1939) 525, t. 37, syn. nov. — Type: *Klug 1268* (holo F; iso NY, US), Peru, Loreto, Mishuyacu, near Iquitos, 100 m, Apr. 1930.

Guatteria calliantha R.E.Fr. (1938) 715; (1939) 429, syn. nov. — Type: *Tessmann 5164* (holo B; iso B, NY, S), Peru, Loreto, Upper Amazon River, Lower Itaya River, Soledad, 110 m, 6 June 1925.

Guatteria juninensis R.E.Fr. (1938) 716; (1939) 387, f. 12d, syn. nov. — Type: *C. Schunke 267* (holo F 2 sheets), Peru, Junín, Schunke Hacienda, above San Ramón, 1400–1700 m, 8–12 June 1929.

Guatteria ovalifolia R.E.Fr. (1939) 328, syn. nov. — Type: *A.C. Smith 3449* (holo S; iso B, F, G, K, MO, NY, P, U), Guyana, NW slopes of Kanuku Mts, in drainage of Moku-Moku Creek (Takutu tributary), 150–400 m, Apr. 1938.

Guatteria collina R.E.Fr. (1939) 381, syn. nov. — Type: *Goudot s.n.* (holo K; iso P), Colombia, 'Savana grande'.

Guatteria buchtienii R.E.Fr. (1939) 388, syn. nov. — Type: *Buchtien 699* (holo S; iso NY, US), Bolivia, La Paz, Mapiri Region, San Carlos, 850 m, 18 Dec. 1926.

Guatteria lasiocalyx R.E.Fr. (1939) 388, syn. nov. — Type: *Bang 583* (holo UPS; iso BM, BR, C, E, F, G, K, L, M, MO, NY 2 sheets, S, U, US, W), Bolivia, La Paz, Yungas, anno 1890.

Guatteria rhamnoides R.E.Fr. (1939) 389, syn. nov. — Type: *Krukoff 5707* (holo S; iso BM, F, G, K, M, MO, NY, RB, U, US), Brazil, Acre, Basin of Rio Purus, near mouth of Rio Macauã ('Macauhan'), tributary of Rio Yacu, 27 Aug. 1933.

Guatteria pteropus Benth. var. *angustior* R.E.Fr. (1939) 420, syn. nov. — Type: *Spruce 1342* (holo K; iso F 2 sheets, K, P), Brazil, Amazonas, Manaus ('Barra'), Feb. 1851.

Guatteria pteropus Benth. var. *cinerea* R.E.Fr. (1939) 420, syn. nov. — Type: *Ducke RB 29018* (holo S; iso MO, RB), Brazil, Amazonas, Parintins, between Paraná de Ramos and Tracajá, 11 Jan. 1936.

Guatteria olivacea R.E.Fr. (1939) 423; Maas et al. (2007) 641, syn. nov. — Type: *Krukoff 6853* (holo S; iso BM, BR, F, G, K, MO, NY, U, US), Brazil, Amazonas, Basin of Rio Madeira, Mun. Humaitá, near Livramento, 12 Oct.–6 Nov. 1934

Guatteria obliqua R.E.Fr. (1939) 424, f. 14e, syn. nov.. — Type: *J.G. Kuhlmann 643* = *RB 24280* (holo S; iso F, INPA, RB, SPF), Brazil, Rondônia, Rio Abunã ('Abunam'), 17 Oct. 1923.

Guatteria occidentalis R.E.Fr. (1939) 430, f. 15b, syn. nov. — Type: *Rose et al. 23429* (holo S; iso F, GH, NY), Ecuador, El Oro, Portovelo, '984 m', 6–15 Oct. 1918.

Guatteria chrysopetala (Steud.) Miq. var. *major* R.E.Fr. (1939) 435, f. 16a, b. — Type: *Ducke RB 19612* (holo S, iso RB), Brazil, Pará, Ôbidos, 19 Sept. 1927.

Guatteria chrysopetala (Steud.) Miq. var. *tenuipes* R.E.Fr. (1939) 435. — Type: A*nonymous collector 239*, *249* (syn UPS, not seen), French Guiana, without location.

Guatteria sagotiana R.E.Fr. var. *gracilior* R.E.Fr. (1939) 437. — Type: *Poiteau s.n.* (holo K), French Guiana, without location, July 1824.

Guatteria sagotiana R.E.Fr. [var. *sagotiana*] (1939) 437. — Type: *Sagot 1263 p.p.* (holo K 2 sheets), French Guiana, Roura, anno 1859.

Guatteria gracilipes R.E.Fr. (1939) 438.— Type: *Krukoff 1156* (holo S; iso G, NY, P, U), Brazil, Pará, Upper Cupari ('Cupary') River, between Xingu and Tapajós Rivers, 16 Sept. 1931.

Guatteria longestipitata R.E.Fr. (1939) 438, f. 17a, b, syn. nov. — Type: *Ducke RB 19613* (holo S; iso RB), Brazil, Pará, Juruti Velho, 23 Dec. 1926.

Guatteria parviflora R.E.Fr. (1939) 440, f. 18a, syn. nov. — Type: *J.G. Kuhlmann RB 24263* (holo S), Brazil, Pará, Santa Júlia, Serra de Parintins, 18 Mar. 1924.

Guatteria lanceolata R.E.Fr. (1939) 443, f. 18b, c, syn. nov. — Type: *Krukoff 5950* (holo S; iso BM, F, G, K, MO, NY, S, U, US 2 sheets), Brazil, Amazonas, Mun. Borba, near Urucurituba, 4–6 Sept. 1934.

Guatteria elliptica R.E.Fr. (1939) 445, f. 19c, d, syn. nov. — Type: *Glaziou 9605* (holo C; iso K, P 2 sheets), Pará, Santarém (?) ('Rio de Janeiro, São Fidelis'), 18 Feb. 1876.

Guatteria umbonata R.E.Fr. (1939) 447, f. 16e, g, syn. nov. — Type: *Ducke RB 19614* (holo S), Brazil, Pará, Santarém, 'loco Mahicá', 25 Mar. 1916.

Guatteria gamosepala R.E.Fr. (1939) 528, f. 37a–d, syn. nov. — Type: *Krukoff 6047* (holo S; iso BM, BR, F, G, K, MO, NY, U, US), Brazil, Amazonas, Basin of Rio Madeira, Mun. Manicoré, near Santa Fé, 8–11 Sept. 1934.

Guatteria leiocarpa R.E.Fr. (1939) 530, f. 36c, d, syn. nov. — Type: *Krukoff 8995* (holo S; iso BM, BR, F, G, K, MO, NY, P, U, US), Brazil, Amazonas, Mun. São Paulo de Olivença, Basin of Creek Belém, 26 Oct.–11 Dec. 1936.

Guatteria macrocalyx R.E.Fr. (1939) 530, syn. nov. — Type: *Mutis 3705* (holo US), Colombia, without location and date.

Guatteria calimensis R.E.Fr. (1950a) 332, syn. nov. — Type: *Cuatrecasas 16566* (holo S 2 sheets; iso F 3 sheets, U, US), Colombia, Valle del Cauca, La Trojita, 5–50 m, 19 Feb.–10 Mar. 1944.

Guatteria latipetala R.E.Fr. (1957b) 602, syn. nov. — Type: *Schultes 5512* (holo US; iso US), Colombia, Vaupés, Río Macaya, near Cachivera del Diablo and mouth of river, 300 m, May 1943.

Guatteria asplundiana R.E.Fr. (1959a) 24; Erkens et al. (2008) f. 3, pl. 4, syn. nov. — Type: *Asplund 19673* (lecto S, selected by Maas et al. 1994; isolecto G, P), Ecuador, Pastaza, Mera, near Manguyacu, 14 Dec. 1956.

Guatteria wessels-boerii Jans.-Jac. (1970) 336, pl. 1. — Type: *Wessels-Boer 1302* (holo U; iso K, NY, WAG, Z), Suriname, near confluence of Paloemeu and Tapanahoni Rivers, 15 Apr. 1963.

Guatteria sp. 10 Chatrou et al. (1997) 111.

Tree or shrub 1–45 m tall, 5–75 cm diam. Young twigs densely to sparsely covered with appressed (or rarely erect) hairs, soon glabrous. *Leaves*: petiole 4–30 mm long, 1–6 mm diam; lamina chartaceous to coriaceous, narrowly elliptic, sometimes elliptic or narrowly obovate, 7–35(–45) cm long, 3–14(–18) cm wide (leaf index 1.5–3.5(–5)), not verruculose, dull to shiny, grey to brown above, greyish brown to brown below, glabrous or primary vein variably covered with appressed or rarely erect hairs above, sparsely to rather densely (rarely densely) covered with appressed hairs below, base acute, shortly to long-attenuate, sometimes obtuse or even cordate, apex acuminate (acumen 5–25 mm long), rarely acute, primary vein slightly impressed to flat above, sometimes keeled below, secondary veins distinct, impressed to flat above, 10–25 on either side of primary vein, smallest distance between loops and margin 1–5 mm, tertiary veins flat, slightly raised or slightly impressed above, reticulate to percurrent. *Flowers* in 1–3(–5)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–35(–55) mm long, 1–2 mm diam, fruiting pedicels 2–4 mm diam, densely to sparsely covered with appressed (to semi-erect or erect) hairs, articulated at 0.2–0.5 from the base, bracts 5–7, soon falling, the 2 upper ones elliptic to broadly elliptic, to 6(–10) mm long (one upper bract exceptionally foliaceous and c. 40 by 10 mm), middle bract elliptic, c. 5 mm long, lower bracts elliptic to ovate or broadly so, 1–2 mm long; flower buds depressed ovoid, apex obtuse or acute; sepals free, rarely basally connate, broadly to shallowly ovate-triangular, 4–10 by 4–10 mm, reflexed or appressed, outer side densely covered with

appressed to erect hairs; petals green, yellow, cream or white, sometimes glaucous in vivo, oblong-elliptic, 10–40{–50} by 5–20 mm, outer side densely covered with appressed hairs; stamens 1–2 mm long, connective shield hairy, papillate, or glabrous, umbonate to flat. *Monocarps* 5–100, green, maturing black to purple-black in vivo, black to brown, sometimes glaucous in sicco, ellipsoid to subglobose, 7–20 by 4–15 mm, sparsely covered with appressed hairs, soon glabrous, apex rounded to apiculate (apiculum < 1 mm long), wall 0.1–1{–4} mm thick, stipes 6–30 by 0.5–2{–3} mm. *Seed* ellipsoid to subglobose, 6–12 by 4–8 mm, pale to dark brown, pitted to smooth, sometimes rugose, raphe raised.

Distribution — Colombia (Amazonas, Antioquia, Boyacá, Cauca, Chocó, Guainía, Meta, Valle del Cauca, Vaupés, Vichada), Venezuela (Amazonas, Bolívar, Delta Amacuro, Zulia), Guyana, Suriname, French Guiana, Ecuador (Azuay, Carchi, Esmeraldas, Morona-Santiago, Napo, Pastaza, Santiago-Zamora, Sucumbios, Zamora-Chinchipe), Peru (Amazonas, Cajamarca, Cusco, Huánuco, Loreto, Madre de Dios, Oxapampa, Pasco, San Martín, Ucayali), Brazil (Acre, Amapá, Amazonas, Maranhão, Mato Grosso, Pará, Rondônia), Bolivia (Beni, Cochabamba, La Paz, Pando, Santa Cruz).

Habitat & Ecology — In non-inundated lowland, premontane or montane forest, often on clayey soil. At elevations of 0–2800 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Bolivia: Chia (*de Michel et al. 590*), Chirimoya del monte (*de Michel et al. 590*), Chocolatillo negro (*D.N. Smith et al. 13252*, *13749*), Laurel macho (*deWalt et al. 121*), Maurel canelón (*Endara s.n.*), Midha dhahua (Tacana) (*Bourdy 1740*, *de Walt et al. 121*, *Serato 58*), Palo pancho verde (*Serato 58*), Piraquina (*Guillén & Roca 2494*), Piraquina de barbecho (*Meneces 2087*), Piraquina negra (*Quevedo et al. 90*, *D.N. Smith et al. 14128*). Brazil: Envira (*Krukoff 6411*, *Pacheco et al. 120*), Envira-cajú (*Figueiredo 803*), Envira-flor-grande (*Fróes 11638*), Envira-fofa (*Daly et al. 6878*), Envira-manga-de-anta (*Pardo et al. 106*), Envira-preta (*Daly et al. 4331*, *Fróes 11787*, *M.J.P. Pires et al. 868*, *Rosa et al. 1750*, *2768*), Envireira (*H.C. Lima et al. 2716*, *Rodrigues 233*), Envireira-da-birida (*Sobel et al. 4615*), Invira (*Krukoff 6047*), Invireira (*Campbell et al. 9694*), Seiseiunahi (Yanomami name) (*Milliken 1706*, *2089*), Taiwi'i (*Balée & Ribeiro 1742*). Colombia: Cargadero (*Cuatrecasas 16253*, *Faber-Langendoen & Rentería A. 1368*, *Gentry et al. 53678*, *Monsalve B.1482*, *1500*, *Triana s.n.*), Cargadero negro (*Cuatrecasas & Patiño 27452*), Garrapato (Tick tree) (*Dawe 946*, *Fonnegra et al. 3135*, *3140*), Guasco dulce (*Zarucchi 3271*), Kïbojïu dujeko (Muinane name) (*Murillo A. & Rodríguez 561*), Zuto (*Betancur et al. 6811*). Ecuador: Cargadera negra (*C. & E. Aulestia 899*), Chiwiachim (Shuar name) (*Aulestia & Gonti 1915*), Fandicho (Cofán name) (*Cerón 20720*, *41738*), Fanicho (Cofán name) (*Cerón 20901*), Gañitahue (Huaorani name) (*Aulestia & Gonti 1795*), Mucataremon (Huaorani name) (*Aulestia et al. 1044*), Neayatio (Secoya name) (*Freire et al. 2861*), Oñitahua (Huaorani name) (*Aulestia & Bainca 3088*), Oñitahue (Huaorani name) (*Aulestia et al. 1965*, *3206*), Oñitahuemo (Huaorani name) (*Aulestia & Quihuiñamo 3173*), Shapattovo (Cofán name) (*Cerón 20895*), Ucucha anona (Quichua name) (*Gudiño & Andi 2040*). French Guiana: Iliwa (Wayana name) (*Fleury 1475*), Iwi (Wayãpi name) (*Prévost & Grenand 1020*), Iwilusi (Wayãpi name) (*de Granville 2633*), Mamayavé/Maman yawée (Creole name) (*de Granville B.4614*, *B.5125*,

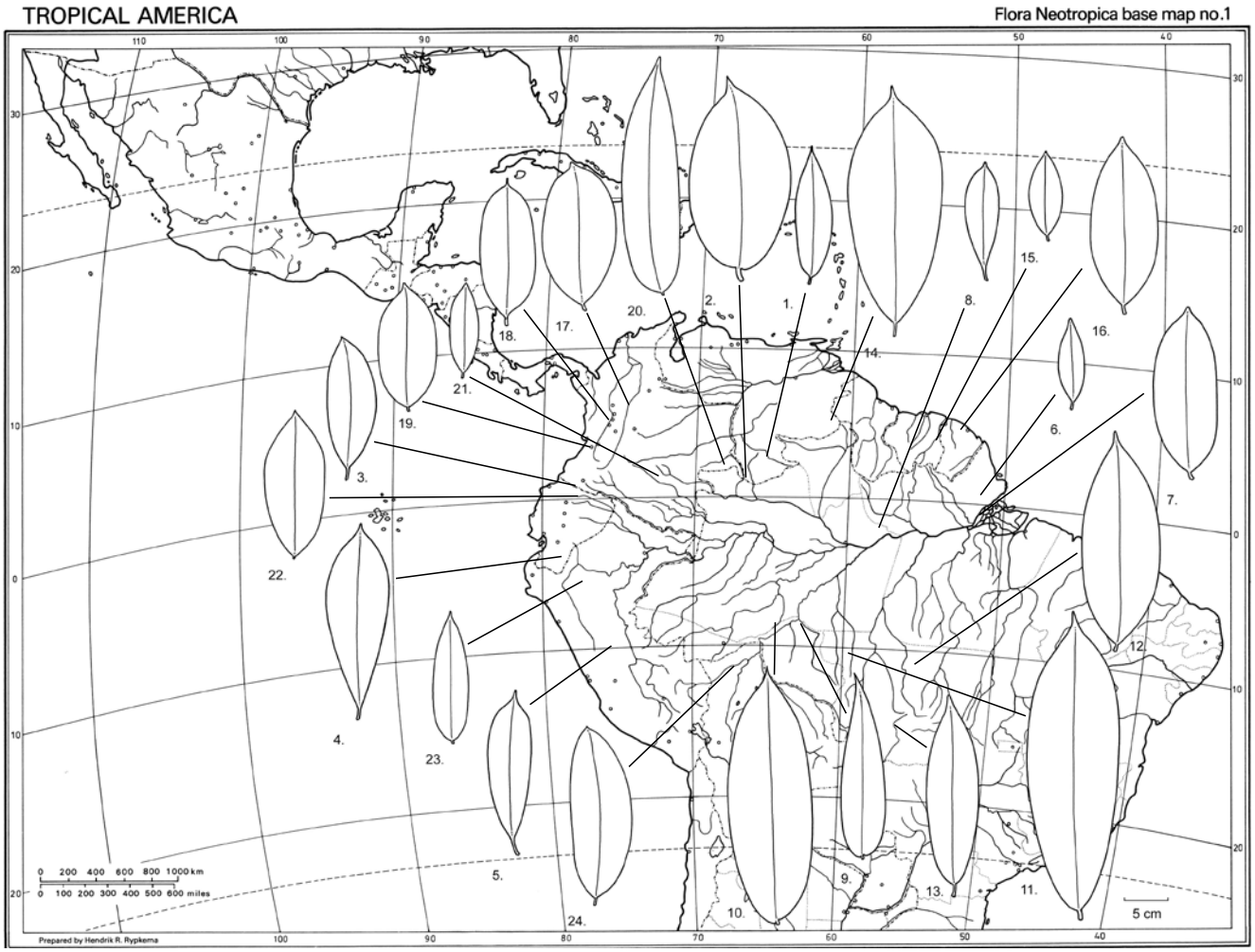


Fig. 63 *Guatteria punctata* (Aubl.) R.A.Howard. Analysis of leaf shapes.

Oldeman 1579, *B.3142*, *B.3477*), Mamayawé commun (Creole name) (*Oldeman 2841*), Pina? ipinu (Wayãpi name) (*de Granville B.5156*), Pinaou (Galibi Carib name; see Aublet (1775) 615). Guyana: Arara (Arawak name) (*Tutin 360*), Black Kuyama (Arawak name) (*Sandwith 406*), Black maho (Creole name) (*Van Andel et al. 666*), Kuyama (Carib name) (*Van Andel et al. 666*), Yarayara (Carib name) (*Van Andel et al. 1127*). Peru: Amarillo (*D.N. Smith & Pretel 1491*, *1549*), Anonilla (*D. Smith 2088*), Anonilla blanca (*Pariona et al. 23*, *941*), Auca hicoja (*Schunke V. 14100*), Carahuasca (*Angulo 5a*, *Ellenberg 2459*, *Hartshorn 1683*, *Kröll Saldaña 674*, *Reynel R. 3*, *D.N. Smith et al. 1203*), Carahuasca negra (*Gutiérrez R. et al. 206*), Caravasca (*Tessmann 3235*), Muraya (Shuar name) (*Neill & Manzanares 13144*), Wámpuyais (Shuar name) (*Kayap 395*), Yaïs (Shuar name) (*C. Díaz et al. 7230*, *7237*, *R. Rojas et al. 393*), Yanahuasca (*Schunke V. 2065*), Yana huasca (*Graham 2578*), Zoro caspi (*Spichiger et al. 1773*), Zorro caspi (*Daly et al. 5727*). Suriname: Arara (Arawak name), Baaka pau, mamaai (Saramaccan name), Blaka paw (Saramaccan name) (*van Donselaar 2078*), Boesi-soensaka (S), Boszuurzak (Sranang name) (*Elburg*, *LBB 9881*, *Lindeman 3646*, *4982*, *6151*, *6759*, *Schulz*, *LBB 8250*, *Vreden*, *LBB 13711*), Koeli koejokoe (Arawak name) (*Stahel s.n.*), Krabietakaka (Sranang name) (*BW 470*), Panta (Sranang name) (*van Donselaar 1806*, *Lindeman 6809*), Pedrekoe pisi (Sranang name). Venezuela: Annoncillo (*Steyermark 88270*), Majagua (*Delgado 836*, *Velazco 1969*), Majagua blanca (*Marcano-Berti 68-979*), Majagua hoja larga (*Liesner 6188*), Majagua negra (*Marcano-Berti et al. 39-1-77*), Majagua verde (*Aymard C. 9793*, *Liesner 7055*), Wosewayek (*Hernández et al. 29*, *118*), Yarayara amarilla (*Blanco 332A*), Yarayara morada (*Marcano-Berti 422*, *622*).

Uses — Suriname: Edible fruits, leaves in herbal bath (*Van Andel 5354*). Wood used for boards (*Van Andel & Poeketi 4807*).

Notes — In 1939 Robert Fries described sect. *Pteropus* as one of the 30 sections he then recognized in the genus *Guatteria*. As the name 'Pteropus' ('winged foot') already suggests, one of the features of this section is the attenuate and almost winged leaf base ('Blätter an der Basis zugespitzt, meist nach unten keilförmig verschmälert'; in Latin: 'Folia vulgo decurrentia'). Another main feature of sect. *Pteropus* consists in the indument, which is almost always composed of appressed hairs (except for *G. sylvicola* in which the hairs are often erect). The section is mainly distributed in the Guianas and the Amazon Region.

Section *Pteropus* originally included 16 species, increased after that to 20 species (Fries 1959b). The species were keyed out by Fries (1939) almost exclusively by leaf features such as leaf shape, leaf base, leaf apex, leaf indument and in a few cases pedicel length.

After extensive comparison of much more material than Fries had at his disposal as late as 1959, we can now accept *G. elata*, *G. elongata* (only known from the type) and *G. modesta* (including 4 of Fries' species: *G. chlorantha*, *G. geminiflora*, *G. glaberrima* and *G. tessmannii*). The remaining species together with a number of other species not classified by Fries in sect. *Pteropus* all form the *G. punctata* complex which will be discussed now.

This complex includes most of the species of sect. *Pteropus*, namely *G. atra*, *G. axilliflora*, *G. calliantha*, *G. chrysopetala*, *G. guentheri*, *G. obliqua*, *G. occidentalis*, *G. olivacea*, *G. ovalifolia*, *G. poeppigiana*, *G. pteropus* and *G. sylvicola*. We checked the material of all these above mentioned species and tried to find some distinguishing features. Despite many trials we were unable to delimit these species convincingly. The differences found in the leaves, like shape of the leaf base, did not hold: the variation in the shape of the leaf base simply is too variable in this complex.

1. Typically, *G. pteropus* and *G. olivacea* show a strongly attenuate leaf base, but in much material of Brazil, Peru, Ecuador and Venezuela one can observe attenuate, acute, to obtuse or even cordate leaf bases. The extremes, in other words, may look very different, but they are connected by all kinds of intermediate forms (see also Fig. 63), and we could not maintain them as distinct species.
2. Leaf colour in dried material in this complex is also quite variable: brown leaves are most commonly found, but greyish colours in various shades as well as transitional colours are also encountered.
3. Leaf size is highly variable in this complex (Fig. 63), large leaves often abound (among others in Peru, the Brazilian state of Acre and elsewhere), vs very small and narrow leaves (among others in the Brazilian state of Pará and in some parts of Suriname).

We also checked features of inflorescence, flowers and fruits of this complex, only to find great variation, too, and hardly useful differences.

It is worth noting that seeds of all species involved in this complex appear remarkably similar, being of almost equal size and mostly smooth to only slightly pitted.

Fries (1939) distinguished in *Guatteria* a sect. *Tylodiscus* with as main feature an umbonate connective shield ('Staubblattschilde mit einem centralen Umbo'). In that section he included 20 different species, several of which occur in the Guianas and adjacent Brazil, namely *G. chrysopetala*, *G. gracilipes* and *G. sagotiana*. After an intensive study of Guianan *Annonaceae* we came to the conclusion that these species are part of one complex species, namely *G. punctata*. The next logical step for us then was to compare the concepts of *G. pteropus* and *G. punctata* more closely. The feature of the presence of an umbo on the connective shield, striking though it may be, is not constant, the centre of the connective shield varying from distinctly elevated (= umbonate) to merely a non-elevated area which still might stand out as such to not at all. This being so, the main distinguishing feature of sect. *Tylodiscus* appeared not to be constant. Furthermore, we did not find good differences in leaves, flowers and fruits to be able to maintain the two entities as separate species. Therefore we propose herewith to unite both species under the oldest name, namely *G. punctata*.

In a late stage of our revision we compared *G. punctata* with species of sect. *Guatteria.* In an earlier publication (Maas & Westra 2010), we already united all species of this section, namely *G. buchtienii*, *G. coeloneura*, *G. juninensis*, *G. lasiocalyx*, *G. pleiocarpa* and *G. rhamnoides* under one species, namely *G. glauca*. Although *G. glauca* shows some slight differences with *G. punctata* in a narrower sense, namely an indument often composed of erect hairs and often basally connate sepals, we found material with erect hairs and slightly connate sepals in *G. punctata* as well. For us there remained little else, and much to our reluctance, than to unite *G. glauca*, mainly restricted to Bolivia and Peru, with *G. punctata*.

Then, during the last phase of our revisionary work, we had to deal with a group of species mainly restricted to the Pacific coast of Colombia and Ecuador (among others, *G. cargadero* and *G. asplundiana*). Notable features in this group are often somewhat larger monocarps (in *G. asplundiana*) and relatively broad and leathery leaves (in *G. cargadero*). Here, again, distinctions are not as sharp as they seem at first, with both monocarps and leaves being variable, but as in all other features of leaves and flowers there were no great differences with *G. puncata* we decided, albeit again with much hesitation, to include both concepts in *G. punctata*.

The outcome of this study for the present is: one large species, namely *G. punctata*, covering most parts of tropical South

America (except for SE Brazil). We are fully aware that this decision is quite tentative and we hope that additional studies (including intensive field work and molecular studies) will contribute to a final unraveling of this complex.

131. *Guatteria ramiflora* (D.R.Simpson) Erkens & Maas — Plate 6g, h; Map 27

Guatteria ramiflora (D.R.Simpson) Erkens & Maas (2008) 404. — *Guatteriopsis ramiflora* D.R.Simpson (1982) 305. — Type: *Schunke V. 3924* (holo F; iso COL, F, G 2 sheets, K, MO, P, S, U, US), Peru, San Martín, Prov. Mariscal Caceres, Tocache Nuevo, Quebrada de Ishichimi (Fundo Retiro), 15 Apr. 1970.

Tree 8–45 m tall, 10–40 cm diam; young twigs rather densely covered with appressed hairs, very soon glabrous. *Leaves*: petiole 10–35 mm long, 3–6 mm diam; lamina elliptic to obovate or narrowly so, 15–35 by 6–15 cm (leaf index 1.6–2.6), coriaceous, not verruculose, shiny, greyish to blackish brown above, brown below, sparsely covered with appressed to erect hairs mainly along veins to soon glabrous above, rather densely to sparsely covered with appressed hairs below, base acute to obtuse, strongly attenuate into a winged petiole, apex acuminate (acumen 10–15 mm long), primary vein impressed above, often keeled below, secondary veins distinct, 20–30 on either side of primary vein, impressed above, smallest distance between loops and margin 2–3 mm, tertiary veins slightly raised above, more or less percurrent. *Flowers* in 1–5-flowered inflorescences, in axils of leaves or on leafless branchlets; pedicels 20–30 mm long, 1–2 mm diam, fruiting pedicels 2–4 mm diam, rather densely to finally sparsely covered with appressed hairs, articulated at 0.2–0.6 from the base, bracts 5–7, soon falling, the basal ones broadly elliptic to broadly ovate, c. 2 mm long, the upper ones ellliptic, c. 7 mm long, occasionally foliaceous bracts present, elliptic, c. 25 mm long; flower buds broadly ovoid, slightly pointed or not; sepals free, broadly elliptic-ovate, 7–9 by 5–7 mm, eventually reflexed, outer side densely covered with appressed hairs; petals green, maturing yellowish green to orange-green to brown in vivo, elliptic to broadly elliptic, 15–25 by 9–17 mm, outer side densely covered with appressed, curly hairs; stamens 1.5–2 mm long, connective shield papillate, umbonate to flat. *Monocarps* 50–75, green, maturing black in vivo, black in sicco, ellipsoid, 11–13 by 5–6 mm, glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.2–0.4 mm thick, stipes 20–35 by 0.5–1 mm. *Seed* ellipsoid, 9–12 by 5–6 mm, pale brown, pitted, raphe raised.

Map 28 Distribution of *Guatteria punctata* (●) and *G. reinaldii* (⊙).

Distribution — Amazonian Colombia (Amazonas), Ecuador (Morona-Santiago, Napo, Pastaza), Peru (Cusco, Huánuco, Loreto, Pasco, San Martín, Ucayali), Brazil (Acre).

Habitat & Ecology — In non-inundated, primary forest, rarely in várzea forest (Brazil) or once in campinarana vegetation (Brazil), on white sands, rarely on clayey soil. At elevations of 0–1100 m. Flowering: mainly from September to March; fruiting: throughout the year.

Vernacular names — Brazil: Envira-cajú (*Figueiredo 803*), Envira-da-folha-grande (*Silveira et al. 852*). Ecuador: Chiwiachim (Shuar name) (*M. Aulestia & Gonti 1915*), Oñitahua (Huaorani name) (*M. Aulestia & Bainca 3088*), Oñitahue (Huaorani name) (*M. Aulestia & Gonti 1965*, *M. Aulestia & Quihuinamo 3206*), Oñitahuemo (Huaorani name) (*M. Aulestia & Gonti 3173*). Peru: Auca hicoja (*Schunke V. 14100*), Carahuasca (*Reynel R. 3*).

Note — *Guatteria ramiflora* is well marked by a very long, winged petiole, combined with leaves with a large number of secondary veins, and often percurrent tertiary veins.

132. *Guatteria reinaldii* Erkens & Maas — Map 28

Guatteria reinaldii Erkens & Maas in Erkens et al. (2006) 206, f. 4. — Type: *R. Aguilar et al. 2031* (holo INB; iso U), Costa Rica, Puntarenas, Cantón de Osa, Fila Costeña, 2 km N of Piedras Blancas, near Cerro Anguciana, 900 m, 28 July 1993.

Tree 4–10 m tall, c. 12 cm diam; young twigs rather densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2–4 mm long, 1–2 mm diam; lamina narrowly ovate to narrowly elliptic and slightly falcate, 13–20 by 4–6 cm (leaf index 2.8–3.3), chartaceous, sparsely or not verruculose, shiny, greyish green above and below, glabrous above, but primary vein densely covered with appressed to erect hairs (primary vein may look verrucose by remaining hair bases), sparsely to rather densely covered with appressed hairs below, base obtuse, apex acuminate (acumen 10–15 mm long), primary vein flat above, secondary veins distinct, 6–10 on either side of primary vein, strongly raised above, smallest distance between loops and margin 3–5 mm, tertiary veins strongly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 3–5 mm long, c. 1 mm diam, fruiting pedicels to c. 7 mm long, to c. 3 mm diam, densely covered with appressed, dark brown hairs, articulation not observed, bracts 4–6, soon falling; flower buds depressed ovoid; sepals free, broadly ovate-triangular, c. 6 by 6 mm, appressed, outer side densely covered with appressed, dark brown hairs; petals cream in vivo, broadly ovate-triangular, 8–14 by 8–11 mm, outer densely covered with appressed, dark brown hairs; stamens 2–2.5 mm long, connective shield papillate. *Monocarps* < 10, purple-black in vivo, black in sicco, narrowly ellipsoid, 10–14 by 4–8 mm, sparsely covered with appressed hairs, apex rounded to apiculate (apiculum < 0.5 mm long), wall 1–1.5 mm thick, stipes 1–3 by c. 1 mm. *Seed* ellipsoid, c. 10 by 6 mm, pale brown, pitted, raphe not studied.

Distribution — Costa Rica.

Habitat & Ecology — In forest. At an elevation of c. 900 m. Flowering: July, December; fruiting: July, December.

Vernacular names — Not recorded.

Note — *Guatteria reinaldii* at first sight resembles *G. pudica* but its parts are generally smaller in size. Both species occur in the Osa area and probably are closely related.

133. *Guatteria revoluta* Maas & Westra, *sp. nov.* — Fig. 54f, 64; Map 29

Foliis coriaceis venis secundariis supra impressis marginibus basalis revolutis monocarpiis breviter stipitatis stipitibus monocarpiis non superantibus distincta. — Typus: *Vásquez & Jaramillo 8024* (holo MO; iso U), Peru, Loreto, prov. Maynas, Puerto Almendras, 122 m, 29 Sept. 1986.

Fig. 64 *Guatteria revoluta* Maas & Westra. Flowering branch (*Vásquez & Jaramillo 8024*, isotype U (sheet 1)).

Tree 6–32 m tall, 25–30 cm diam; young twigs rather densely covered with appressed, rarely erect hairs, soon glabrous. *Leaves*: petiole 10–20 mm long, c. 3 mm diam; lamina narrowly elliptic to narrowly obovate, 17–35 by 6–14 cm (leaf index 2.2–3), coriaceous, not verruculose, slightly shiny, dark brown, sometimes greyish brown above, brown below, glabrous above, sparsely covered with appressed, rarely erect hairs below, base acute to attenuate, basal margins mostly stongly revolute, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins distinct, 15–25 on either side of primary vein, impressed above, smallest distance between loops and margin 3–6 mm, tertiary veins flat to slightly raised above, reticulate to slightly percurrent. *Flowers* in 1–2(–several)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels c. 10 mm long, c. 2 mm diam, fruiting pedicels to c. 15 mm long, 2–5 mm diam, rather densely to sparsely covered with appressed hairs, articulated at 0.3–0.4 from the base, bracts 5–7, soon falling, not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–7 by 6–7 mm, reflexed, outer side densely covered with appressed hairs; petals green, maturing cream or yellow to reddish yellow in vivo, elliptic to obovate, 10–25 by 6–15 mm, outer side densely covered with appressed hairs; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* 25–75, green, maturing black in vivo, brown to black in sicco, ellipsoid, 10–15 by 7–8 mm, sparsely covered with appressed hairs, apex rounded to apiculate (apiculum < 1 mm long), wall 0.2–0.4 mm thick, stipes 3–5(–20) by 1 mm. *Seed* ellipsoid, 9–11 by 5–6 mm, dark brown, pitted to smooth, raphe raised.

Distribution — Amazonian Peru (Loreto).

Habitat & Ecology — In non-inundated forest, on sandy to clayey soil. At elevations of 100–150 m. Flowering: May, November, September; fruiting: January, March, July, September, October.

Vernacular names — Peru: Anonilla (*J. Ruíz 1075*), Carahuasca (*Díaz M. et al. 88*, *Simpson 765*), Carahuasca negra (*Gutiérrez R. 206*).

Other specimens examined. Peru, **Loreto**, Nauta, *Arévalo & Díaz M. 99* (AMAZ, U); Prov. Maynas, Puerto Almendras, 100 m, *Díaz M. et al. 88* (AMAZ, U); Prov. Maynas, road from Nauta to Iquitos, 150 m, *Grández & Ruíz 2171* (U); Prov. Maynas, Puerto Almendras, Arboretum UNAP, 122 m, *Grández & Jaramillo 4977* (MO, U); Prov. Maynas, Distr. Alto Nanay, Santa Maria de Nanay, 150 m, *Gutiérrez R. 206* (U); Allpahuayo, 20.5 km S of Iquitos, *Maas et al. 8192* (U); Prov. Maynas, Distr. Iquitos, Quebrada Aucaya, 15 m, *Rimachi Y. 369* (MO); Prov. Maynas, Ninarumi, *J. Ruíz 1075* (AMAZ, U); Prov. Maynas, Distr. Alto Nanay, Santa Maria de Nanay, *Simpson 765* (K, MO); Prov. Maynas, Puerto Almendras, 122 m, *Vásquez & Jaramillo 7584* (MO, U); Nauta, km 5 of road from Nauta to Iquitos, 200 m, *Vásquez & Arévalo 9000* (MO, U); Prov. Maynas, Indiana, Yanamono, Rio Amazonas, 116 m, *Vásquez & Jaramillo 11105* (MO, U); prov. Maynas, Puerto Almendras, Río Nanay, 122 m, *Vásquez et al. 13754* (MO, U); Prov. Maynas, Allpahuayo, Estación Experimental del Instituto de Investigaciones de la Amazonía Peruana (IIAP), 150–180 m, *Vásquez et al. 14384*, *14797*, *16322* (MO, U).

Notes — *Guatteria revoluta*, a narrow endemic of the Iquitos region, is recognizable by a combination of coriaceous leaves with impressed secondary veins, revolute basal leaf margins, and shortly stipitate monocarps, the stipes not exceeding the monocarps in length.

Ruíz, *J. 1075* (U) from Peru, Loreto, Ninarumi, may belong here but is aberrant in having stipes up to 10 mm long.

Vásquez & Jaramillo 13267 (MO, U) from Peru, Loreto, Prov. Maynas, Sargento Lores, Esperanza (Río Tahuayo), 120 m, and *Gentry et al. 39690* (AAU, MO, NY, U) from Peru, Loreto, Prov. Maynas, Yanamomo Tourist Camp, Río Amazonas, between Indiana and mouth of Río Napo, 130 m, fit this species quite well by their revolute basal leaf margins and shortly stipitate fruits. They are very different, however, in having an indument of erect instead of appressed hairs both on the leafy twigs and lower side of the lamina!

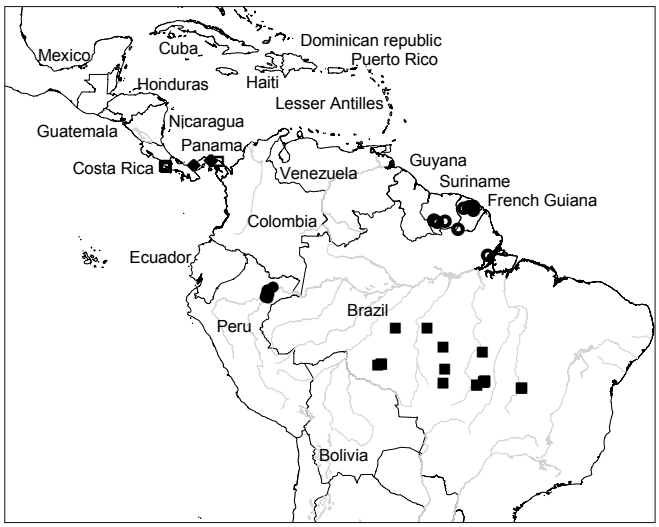
Vásquez & Jaramillo 9434 (MO) from Peru, Loreto, Maynas, Iquitos, km 42 of road from Iquitos to Nauta, 130 m, differs by an indument of erect hairs and, moreover, by much longer stipes 10–20 mm long and pointed monocarps (containing abortive seeds).

134. *Guatteria richardii* R.E.Fr. — Map 29

Guatteria richardii R.E.Fr. (1939) 440. — Type: *L.C. Richard s.n.* (holo P), French Guiana, Kourou River ('in ripis fluvii Kourou').

Guatteria montis-trinitatis Scharf in Scharf et al. (2006b) 548, f. 3, syn. nov. — Type: *De Granville et al. 5947* (holo U; iso B, BR, CAY, G, K, NY, P, US), French Guiana, Montagne de la Trinité, 350 m, 13 Jan. 1984.

Tree 2–12 m tall, 1.5–5 cm diam; young twigs densely covered with erect, brown hairs, soon glabrous. *Leaves*: petiole 2–6 mm long, 2–4 mm diam; lamina narrowly elliptic to narrowly ovate, 10–34 by 4–10 cm (leaf index 2.3–4.4), chartaceous to thinly coriaceous, not verruculose, dull, greyish above, greyish to greenish brown below, densely covered with appressed, brown hairs above, but very soon glabrous, except for the primary vein covered with a row of erect, brown hairs, densely covered with erect, pale reddish brown hairs below, base acute to obtuse, apex acuminate (acumen 10–20 mm long), primary vein impressed above, secondary veins distinct, 10–15 on either side of primary vein, flat to slightly raised above, smallest distance between loops and margin 2–4 mm, tertiary veins flat or slightly raised above, reticulate to percurrent. *Flowers* in 1–3(–4)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–25 mm long, 1–1.5 mm diam, fruiting pedicels to c. 2 mm diam, densely covered with erect, brown hairs, articulated at 0.2–0.6 from the base, bracts 4–5, soon falling, lower bracts very broadly ovate, c. 2 mm long, uppermost bracts not seen; flower buds broadly ovoid; sepals free, broadly ovate-triangular, 6–8 by 5–7 mm, apex reflexed, outer side densely covered with erect, brown hairs; petals yellow in vivo, narrowly elliptic to ovate, 7–15{–26} by 5–9{–14} mm, outer side densely covered with erect, brown hairs; stamens c. 1.5 mm long, connective shield papillate, umbonate or not. *Monocarps* 15–25, black in vivo, black to reddish brown in sicco, ellipsoid, 6–8 by 4–5 mm, glabrous, except for some scattered hairs at the apex, apex rounded to apiculate (apiculum < 0.5 mm long), wall c. 0.2 mm thick, stipes 7–15 by 0.5–1 mm. *Seed* ellipsoid, 7–8 by 5 mm, reddish brown, pitted to transversely grooved, raphe slightly raised.



Map 29 Distribution of *Guatteria revoluta* (●), *G. richardii* (❍), *G. rigida* (■), *G. rostrata* (□) and *G. rotundata* (◆).

Distribution — Suriname, French Guiana, Amazonian Brazil (Amapá).

Habitat & Ecology — In non-inundated or periodically inundated forest, on clayey to sandy soil. At elevations of 0–500 m. Flowering: January, February, July, September to December; fruiting: January, February, April, November.

Vernacular names — Not recorded.

Note — *Guatteria richardii* slightly resembles the French Guianan endemic *G. ouregou* by its erect, brown hairs on the leafy twigs. It differs, however, by the primary vein retaining its indument above for some time (not soon becoming glabrous), yellow instead of orange to orange-yellow petals, and by much smaller monocarps (6–8 vs 8–15 mm long).

135. *Guatteria rigida* R.E.Fr. — Fig. 54g, 65; Map 29

Guatteria rigida R.E.Fr. (1906) 8, t. 1, f. 1, 2; (1939) 482. — Type: *Riedel 438* (holo S), Brazil, Mato Grosso do Sul, Rio Pardo, Aug. 1826.

Tree or shrub 1–14 m tall, to c. 25 cm diam; young twigs rather densely covered with appressed hairs, very soon glabrous. *Leaves*: petiole 5–10 mm long, 1–3 mm diam; lamina elliptic to obovate or narrowly so, 7–18 by 3–7.5 cm (leaf index 1.8–3), coriaceous, not or sparsely verruculose, shiny, dark brown to greyish above, brown below, glabrous above, sparsely covered with appressed hairs, mainly along primary vein and margins below, base acute to attenuate, apex rounded, acute, emarginate, or shortly acuminate (acumen to c. 5 mm long), primary vein impressed to flat above, secondary veins distinct, 8–12 on either side of primary vein, raised above, smallest distance between (indistinct) loops and margin 3–4 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 15–30 mm long, 1–1.5 mm diam, fruiting pedicels to c. 3 mm diam, sparsely covered with appressed hairs, soon completely glabrous, articulated at 0.2–0.3 from the base, bracts 5–7, soon falling, not seen; flower buds broadly ovoid; sepals free, broadly ovate-triangular, 4–5 by 4–5 mm, appressed, finally reflexed, outer side rather densely to sparsely covered with appressed hairs; petals yellowish green or cream in vivo, elliptic, 13–35 by 6–15 mm, outer side rather densely covered with appressed hairs, soon more or less glabrous; stamens 1–1.5 mm long, connective shield papillate. *Monocarps* 25–75, green to red in vivo, brown in sicco, ellipsoid or less often narrowly ellipsoid, 6–12 by 4–5 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum 0.5–1 mm long), wall 0.2–0.3 mm thick, stipes 3–8 by 1–2 mm. *Seed* ellipsoid, 7–10 by 4–5 mm, pale brown, pitted, raphe raised.

Distribution — Brazil (southern part of Amazonas, Goiás, Mato Grosso do Sul, Pará, Rondônia).

Habitat & Ecology — In dry or wet cerrado, sometimes in gallery forest, on sandy to rocky soil. At elevations of 100–1000 m. Flowering: March, June, August to December; fruiting: February, April to June, September, October.

Vernacular name — Brazil: Embireira-do-campo (*Ratter et al. 1921*).

Notes — *Guatteria rigida* is one of the few cerrado inhabiting species of *Guatteria*. It is quite characteristic by its thick leaves which mostly have a very prominent secondary and tertiary venation on the upper side. The apex of the lamina is quite variable, varying from obtuse, acute, emarginate to shortly acuminate. It shares several leaf features with another campo rupestris inhabiting species, namely *G. rupestris*. It differs from the latter by having a longer petiole (5–10 vs 2–4 mm long) and pedicels (15–30 vs 10–15 mm long), more monocarps (25–75 vs 10–15) and strongly pitted instead of smooth to slightly rugulose seeds.

Sasaki et al. 'Parcela 2 540' (K) from Brazil, Mato Grosso, Mun. Novo Mundo, growing in forests ('floresta ombrófila densa submontana') shares the leaf features with this species. It differs, however, by much longer monocarps of 14–15 by 5 mm and longer stipes of 12–14 mm long. The seeds appear to be smooth and are markedly different from the rugulose seeds found in *G. rigida* so far. This quite likely represents an as yet undscribed species perhaps allied to *G. rigida*, but more material is needed for further study.

136. *Guatteria rostrata* Erkens & Maas — Fig. 66; Map 29

Guatteria rostrata Erkens & Maas in Erkens et al. (2006) 210, t. 2, f. 5. — Type: *R. Aguilar et al. 3654* (holo U; iso CR, INB, MO), Costa Rica, Puntarenas, Cantón Osa, Reserva Forestal Golfo Dulce, near Rancho Quemado, 200–350 m, 1 Nov. 1994.

Tree 7–20 m tall, 20–60 cm diam, black or grey; young twigs densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 15–20 mm long, 2–3 mm diam; lamina elliptic to obovate or narrowly so, 18–28 by 7–11 cm (leaf index 2.4–2.6), chartaceous, not verruculose, dull, greyish brown above, brown below, glabrous above, rather densely covered with appressed hairs below, base attenuate into a narrowly winged petiole, apex acuminate (acumen 10–20 mm long), primary vein impressed above, secondary veins distinct, 16–19 on either side of primary vein, raised above, smallest distance between loops and margin 3–6 mm, tertiary veins raised above, reticulate. *Flowers* in 1–2-flowered inflorescences on leafless branchlets or in axils of leaves; pedicels 15–35 mm long, c. 1 mm diam, fruiting pedicels to c. 2 mm diam, densely covered with appressed hairs, finally glabrous, articulated at 0.2–0.3 from the base, bracts 5–7, soon falling, not seen; flower buds broadly ovoid; sepals free, broadly ovate-triangular to ovate-triangular, 7–12 by 5–10 mm, spreading, outer side rather densely covered with appressed hairs; petals green or yellowish green to yellow in vivo, unequal, outer ones ovate, 14–22 by 10–15 mm, inner ones oblong-elliptic to ovate, 10–15 by 5–9 mm, outer side densely covered with appressed hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* 5–15, green, maturing red to purple-black in vivo, black in sicco, narrowly ellipsoid, 15–18 by 6–7 mm, sparsely covered with erect hairs, soon glabrous, apex rostrate (beak 1–2 mm long), wall 0.1–0.2 mm thick, stipes 3–10 by c. 1 mm. *Seed* ellipsoid, 13–15 by 4–7 mm, pale brown, transversely grooved to pitted, raphe impressed.

Distribution — Costa Rica.

Habitat & Ecology — In forest. At elevations of 0–700 m. Flowering: May, July; fruiting: February, May, June, November.

Vernacular names — Not recorded.

Field observations — Flowers with strong odour (*Raaijmakers & Rodríguez 87*, Costa Rica).

Note — In the field *G. rostrata* is easily recognized by its black or grey trunk, sometimes with narrow buttresses reaching up to 8 m (*Hammel 16960*). In the field this species superficially resembles *G. amplifolia* somewhat because of its large leaves. In *G. rostrata*, however, the petiole is generally somewhat longer (15–20 by 2–3 mm vs 4–10 by 4–6 mm). Moreover, the monocarps of *G. rostrata* are 5–15 in number, 15–18 by 6–7 mm and rostrate, while *G. amplifolia* has more monocarps (20–40), which are shorter (8–10 by 5–6 mm) and ellipsoid to pyriform, lacking the rostrate apex.

137. *Guatteria rotundata* Maas & Setten — Plate 7a; Map 29

Guatteria rotundata Maas & Setten (1988) 255, f. 11. — Type: *Nee & Tyson 10999* (holo MO; iso EAP, H, NY, RB, U, XAL), Panama, Panamá, Chepo, El Llano-Carti road, 16–18.5 km by road N of Pan American Highway, 400–450 m, 28 Mar. 1973.

Fig. 65 *Guatteria rigida* R.E.Fr. Flowering branch (*Pereira-Silva et al. 5770*, U).

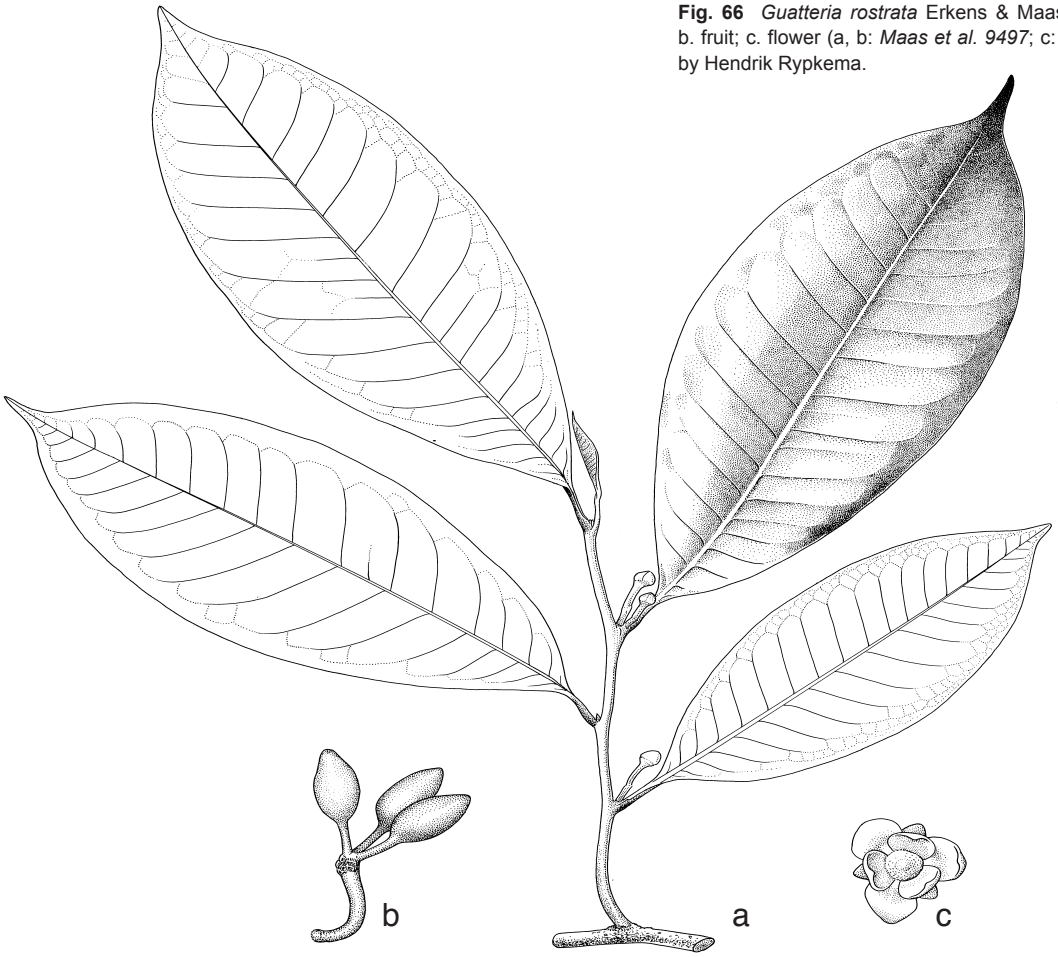


Fig. 66 *Guatteria rostrata* Erkens & Maas. a. Branch with flower buds; b. fruit; c. flower (a, b: *Maas et al. 9497*; c: *Maas et al. 9492*). — Drawing by Hendrik Rypkema.

Tree 5–30 m tall, 20–40 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2–10 mm long, 1–2 mm diam; lamina obovate to obovate-elliptic, 5–14 by 2–6 cm (leaf index 2–2.8), coriaceous, rather densely to sparsely verruculose on both sides, dull, dark brown above, brown below, glabrous above, rather densely to sparsely covered with appressed hairs below, base acute, extreme base attenuate, decurrent along petiole, apex rounded to obtuse, the extreme tip shortly acuminate (acumen 1–5 mm long) or not protruding, primary vein flat above, keeled below, secondary veins distinct, 7–12 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; flowering and fruiting pedicels 4–15 mm long, 1–2 mm diam, rather densely covered with appressed hairs, articulated at 0.2–0.5 from the base, bracts 4–5, soon falling, not seen; flower buds depressed ovoid; sepals basally connate, broadly ovate-triangular, 3–6 by 4–6 mm, appressed, finally reflexed, outer side rather densely covered with appressed hairs; petals green or yellow in vivo, ovate-elliptic to rhombic, 10–17 by 4–12 mm, outer side rather densely to sparsely covered with appressed or erect and curly hairs; stamens 1–2 mm long, connective shield papillate. *Monocarps* 10–25, green in vivo, black in sicco, narrowly ellipsoid, 13–16{–18} by 4–{5–6} mm, glabrous, apex apiculate (apiculum < 0.5 mm long), wall c. 0.1 mm thick, stipes 1–4 by c. 1 mm. S*eed* narrowly ellipsoid, 13–16 by 4–5 mm, pale brown, rugulose.

Distribution — Panama.

Habitat & Ecology — In forest. At elevations of 0–500 m. Flowering: February, April, November; fruiting; February.

Vernacular names — Not recorded.

Note — *Guatteria rotundata* is unique by its leaves, the apex of which is mostly distinctly rounded.

138. *Guatteria ruboides* Maas & Westra, *sp. nov.* — Fig. 54h, 67; Map 30

Species *G. tomentosa* affinis sed monocarpiis fere sessilibus differt. — Typus: *Vásquez* & *Jaramillo 8025* (holo U; iso AAU, MO, NY), Peru, Loreto, Prov. Maynas, Puerto Almendras, 122 m, 29 Sept. 1986.

Guatteria trichoclonia Vásquez (1997) 100; Murillo A. & Restrepo (2000) 116, f. 35, not of Diels (1931).

Tree 8–28 m tall, c. 20 cm diam; young twigs densely covered with long-persisting, erect, stiff hairs ('hirsute') to c. 3 mm long. *Leaves*: petiole 2–3 mm long, c. 1 mm diam; lamina narrowly ovate to narrowly elliptic, 8–12 by 2.5–3 cm (leaf index 2.6–4), chartaceous, not verruculose, dull, dark brown to brownish green above, brown below, rather densely covered with long-persisting, erect to appressed, stiff hairs ('hirsute') to c. 3 mm long above, densely covered with long-persisting, erect, stiff hairs ('hirsute') to c. 3 mm long below, base obtuse, apex acuminate (acumen 5–15 mm long), primary vein flat above, secondary veins indistinct, 10–12 on either side of primary vein, slightly raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves or on leafless branchlets; flowering and fruiting pedicels 20–30 mm long, c. 1 mm diam, densely covered with long-persisting, erect, stiff hairs ('hirsute') to c. 3 mm long, articulated at 0.1–0.3 from the base, bracts 5–6, soon falling or the uppermost often present at flowering time, elliptic or narrowly elliptic, with acuminate apex, to c. 10 mm long; flower buds broadly ovoid, pointed; sepals free, broadly ovate-triangular, 4–6 by 4–5 mm, finally reflexed, apex acuminate, outer side densely covered with long-persisting, erect, stiff hairs ('hirsute') to c. 3 mm long; petals green, maturing yellow in vivo, narrowly ovate-triangular, 12–15 by 3–5 mm, outer side densely covered with appressed

Plate 7 a. *Guatteria rotundata* Maas & Setten. Fruiting branch, flower (insert). – b. *Guatteria rupestris* R.E.Fr. Fruiting branch. – c. *Guatteria scandens* Ducke. Fruit on stem of liana. – d–f. *Guatteria schomburgkiana* Mart. d. Branch with mature flower; e, f. young flower and fruit. – g. *Guatteria sellowiana* Schltdl. Part of flowering branch. – h. *Guatteria sessilicarpa* Maas & Setten. Fruiting branch (a: Ratón, Panama; b: *Simonis & Cordeiro CFCR 4116*; c: *Maas et al. 3600*; d, e: Mabura, Guyana 1988; f: *Maas et al. 7149*; g: *Maas et al. 9842*; h: Cerro Jefe, Panama. — Photos: a: J. Carrion; b: J.E. Simonis; c–f: L.Y.T. Westra; g: P.J.M. Maas; h: J. Harrison.

Fig. 67 *Guatteria ruboides* Maas & Westra. Fruiting branch (*Vásquez & Jaramillo 8025*, isotype AAU).

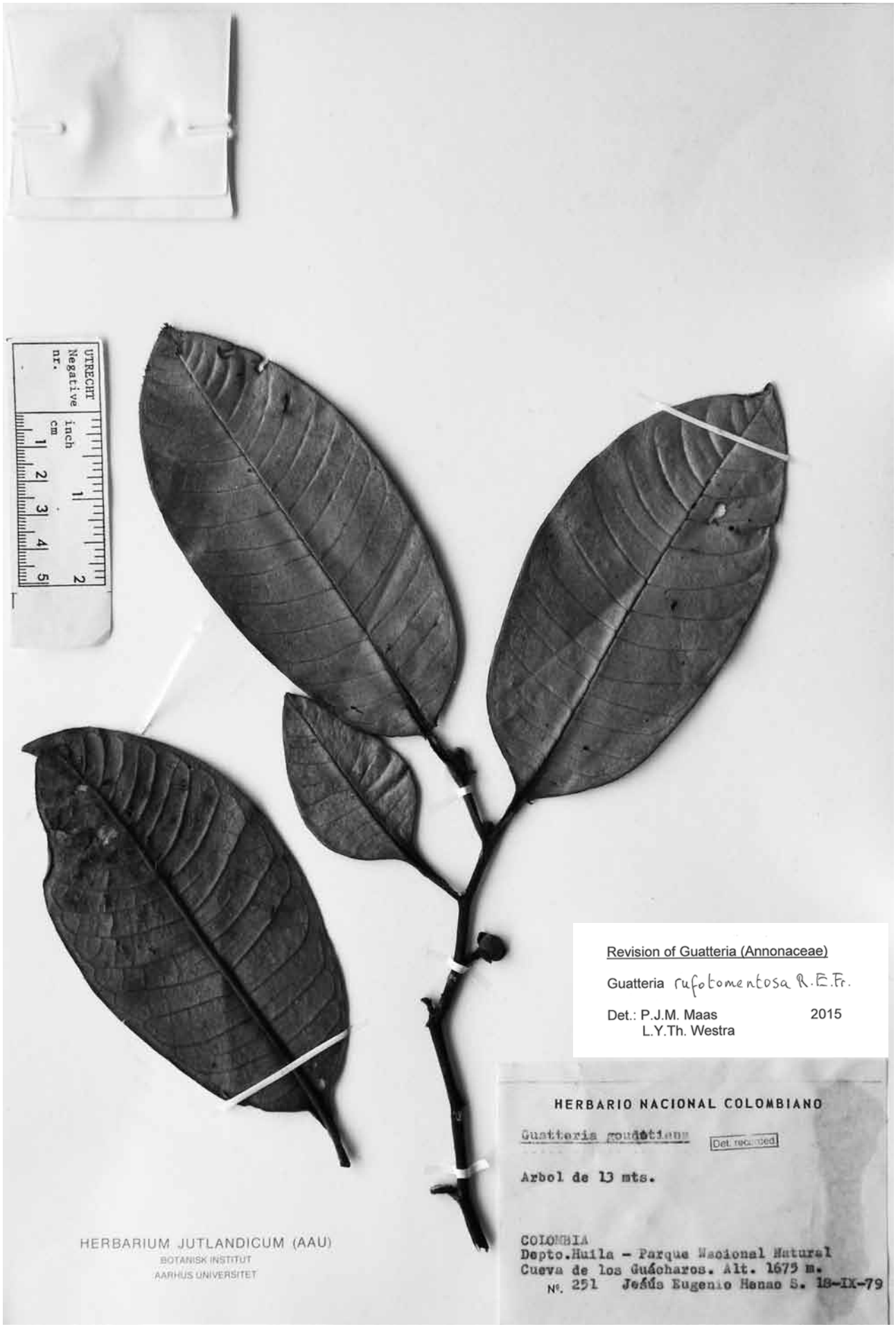


Fig. 68 *Guatteria rufotomentosa* R.E.Fr. Flowering branch (*Henao 251*, AAU).

and erect hairs; stamens c. 1 mm long, connective shield glabrous. *Monocarps* 10–25, green, maturing yellow in vivo, black in sicco, ellipsoid, 5–12 by 3–6 mm (the ripe ones 10–12 by 5–6 mm, somewhat inflated and winged), rather densely to sparsely covered with erect, stiff hairs ('hirsute') to c. 3 mm long, apex rounded, wall 0.1–0.2 mm thick, stipes 0–1 by 0–1 mm. *Seed* ellipsoid, 5–6 by 3 mm, brown, rugulose, raphe not distinct from rest of seed.

Distribution — Amazonian Colombia (Amazonas) and Peru (Loreto).

Habitat & Ecology — In non-inundated forest, on slightly sandy soil. At elevations of 100–350 m. Flowering: March to September; fruiting: July to September.

Vernacular name — Peru: Carahuasca (*Vásquez et al. 9363*, *10549*).

Other specimens examined. Colombia, **Amazonas**, Corregimiento Puerto Santander, La Chorrera, 14 km SW of Araracuara, 350 m, *Cárdenas L. et al. 4195* (COAH, U). – Peru, **Loreto**, Ninarumi, 100 m, *Díaz M. et al. 8* (U); Puerto Almendras (Río Nanay), 122 m, *Grández & Jaramillo 2869* (MO, U), *Grández et al. 4330* (MO), *J. Ruiz 1070* (U), *Vásquez et al. 1400*, *2612*, *8025*, *9363*, *10549* (MO, U); Ninarumi, Río Nanay, *J. Ruiz 1079* (U), *Vásquez & Jaramillo 10789* (MO, U); Mishana, Río Nanay, 150 m, *Vásquez et al. 7534* (MO, U).

Notes — *Guatteria ruboides* clearly belongs in sect. *Trichoclonia* by its indument of persisting, long hairs and pointed flower buds. It is distinct by the sessile monocarps creating a resemblance to a *Rubus* fruit, hence the specific name 'ruboides'.

Several specimens from Colombia may belong here, but one of them (*Vester 111a*) is aberrant in having distinctly stipitate monocarps.

139. *Guatteria rubrinervis* R.E.Fr. — Map 30

Guatteria rubrinervis R.E.Fr. (1952a) 395; Steyerm. et al. (1995) 447, f. 373. — Type: *Forest Department British Guiana 5816 = Wilson-Browne 417* (holo NY; iso FDG, K, NY), Guyana, Kanuku Mts, Wabu-ak, 600 m, Oct. 1948.

Tree 5–18 m tall, to c. 45 cm diam; young twigs densely covered with erect, whitish brown to yellowish brown hairs 1–2 mm long. *Leaves*: petiole 1–4 mm long, c. 1 mm diam; lamina narrowly elliptic, 7–18 by 1.5–4 cm (leaf index 3.5–4.8), chartaceous to thinly coriaceous, not verruculose, shiny, grey to greyish black above, brown to greyish green below, glabrous above, but primary vein densely covered with erect, whitish brown to yellowish brown hairs and the base with some appressed hairs, rather densely covered with appressed to erect, whitish brown to yellowish brown hairs 1–2 mm long below, base acute, apex acuminate (acumen 10–15 mm long), primary vein impressed above, secondary veins distinct, 9–15 on either side of primary vein, raised above, smallest distance between loops and margin 1–3 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels (15–)25–60 mm long, 0.5–1 mm diam, fruiting pedicels to c. 2 mm diam, sparsely covered with erect, golden hairs, articulated at 0.2–0.3 from the base, bracts c. 5, soon falling or upper ones sometimes persisting till flowering time, basal ones (only one seen) elliptic, c. 2 mm long, the 2 upper ones elliptic, 5–10 mm long; flower buds ovoid, pointed; sepals basally connate, broadly ovate-triangular, 6–8 by 5–7 mm, reflexed, outer side rather densely covered with erect, golden hairs; petals green or orange in vivo, narrowly oblong-obovate to oblong-obovate, 8–25 by 5–8 mm, outer side densely covered with appressed hairs; stamens c. 1 mm long, connective shield glabrous. *Monocarps* 20–100, green, maturing purple-black to black in vivo, black in sicco, ellipsoid, 6–8 by 4–5 mm, glabrous, apex rounded to apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 15–25 by 0.5–1 mm. *Seed* ellipsoid, 5–7 by 3–4 mm, shiny, reddish brown, smooth to pitted, raphe not distinct from rest of seed.

Distribution — Amazonian Venezuela (Amazonas, Bolívar, Delta Amacuro), Guyana, Suriname, Brazil (Roraima).

Habitat & Ecology — In non-inundated forest. At elevations of 100–600 m. Flowering: March to June, August, October; fruiting: March, April, June, July.

Vernacular names — Brazil: Envira-preta (*Ratter et al. 5705*). Venezuela: Copito (*Bernardi 7406*), Fruto de burro negro (*Ll. Williams 12938*), Kunwatâ (Yekuana name) (*Rosales et al. 1573*), Maiagua verde (*Chaviel 48*), Majaguillo montañero (*Rosales et al. 1573*).

Notes — *Guatteria rubrinervis* is recognizable by its long pedicels with foliaceous bracts sometimes persisting till flowering time, by erect hairs to c. 2 mm long on most of its parts, and basally connate sepals.

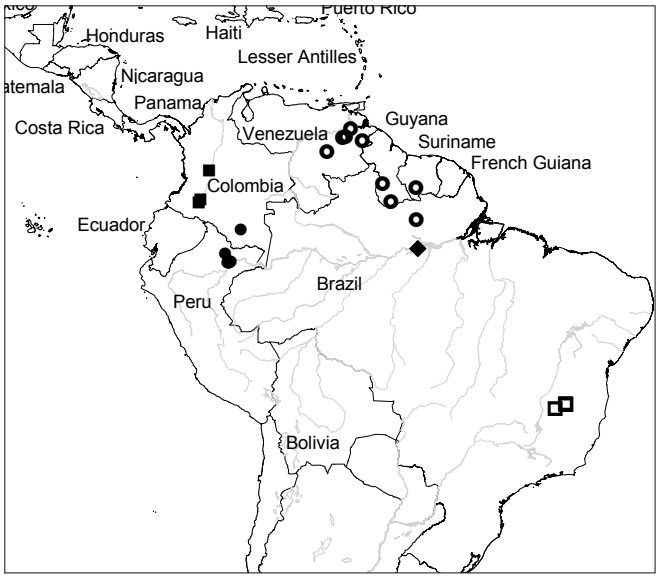
Fries (1952a) placed it in sect. *Stenophyllum*, a section which was united by him (1959b) with sect. *Trichoclonia*.

Guatteria rubrinervis comes quite close to *G. hirsuta* and upon closer research may prove not to be specifically distinct from it. For the time being it can be recognized particularly by the much smoother seed coat (not deeply pitted as in *G. hirsuta*). The pedicels in *G. rubrinervis* are invariably long and slender, whereas pedicels in *G. hirsuta* are generally shorter and more stout (but there is some overlap). Dried leaves in *G. rubrinervis* are blackish or greenish black while in *G. hirsuta* they show normally a rather more brown colour.

140. *Guatteria rufotomentosa* R.E.Fr. — Fig. 68; Map 30

Guatteria rufotomentosa R.E.Fr. (1939) 392, t. 24. — *Guatteria rufa* Triana & Planch. (1862) 35, non Dunal (1817). — Type: *Goudot s.n.* (holo P; iso K), Colombia, Tolima, Ibagué ('Ibagué, prov. Mariquita'), Dec. 1844.

Tree 5.5–13 m tall, or shrub of unknown height and diam (the type collection); young twigs densely covered with erect, brown hairs, soon glabrous. *Leaves*: petiole 5–15 mm long, 2–3 mm diam; lamina narrowly elliptic to elliptic, 14–23 by 6–11 cm (leaf index 2.3–2.8), coriaceous, not verruculose, shiny, grey to greyish brown above, brown to greenish brown below, sparsely covered with erect hairs to glabrous above, densely covered with erect, brown hairs below, base long-attenuate, basal margins revolute, apex acute to acuminate (acumen 10–15 mm long), primary vein impressed above, secondary veins distinct, 15–25 on either side of primary vein, raised above, smallest distance between loops and margin 1–2 mm, tertiary veins



Map 30 Distribution of *Guatteria ruboides* (●), *G. rubrinervis* (⭘), *G. rufotomentosa* (■), *G. rupestris* (□) and *G. sabuletorum* (◆).

Fig. 69 *Guatteria saffordiana* Pittier. Fruiting branch (*Riina et al. 265*, U).

strongly raised to flat above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 5–25 mm long, 2–3 mm diam, fruiting pedicels 10–40 mm long, 2–3 mm diam, densely covered with erect, brown hairs, articulated at 0.3–0.5 from the base, bracts 6–7, soon falling, the 2 upper ones 5–8 mm long; flower buds depressed ovoid to subglobose; sepals free, broadly ovate-triangular, 5–8 by 6–10 mm, appressed, outer side densely covered with appressed hairs; petals colour not recorded, broadly ovate to ovate, 8–11 by 5–10 mm, outer side densely covered with appressed hairs, inner side strongly vertically ridged; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* c. 25, colour in vivo unknown, black in sicco, ellipsoid, 9–10 by 5–6 mm, sparsely covered with appressed hairs, apex apiculate (apiculum < 1 mm long), wall 0.2–0.3 mm thick, stipes c. 2 by 1.5 mm. *Seed* ellipsoid, c. 10 by 6 mm, dark brown, strongly rugose, raphe not distinct from rest of seed.

Distribution — Colombia (Huila, Tolima).

Habitat & Ecology — In oak forests ('robledales') (*Trigobalanus excelsa*). At elevations of 1000–1675 m. Flowering: January, February, September, December; fruiting: September.

Vernacular names — Not recorded.

Note — *Guatteria rufotomentosa* is only known from a few collections gathered in the Colombian states of Tolima and Huila, respectively. It comes closest to *G. carchiana* from montane forests in Ecuador. For the differences see under that species.

141. *Guatteria rupestris* Mello-Silva & Pirani — Plate 7b; Map 30

Guatteria rupestris Mello-Silva & Pirani (1994) 146, f. 1, 2. — Type: *Pirani et al. CFCR 12752* (holo SPF 3 sheets; iso K, MBM, MO, NY, U), Brazil, Minas Gerais, 2 km from Itacambira, on road to Juramento, 14 Dec. 1989.

Shrub or small tree 1–4 m tall, diam not recorded; young twigs sparsely covered with appressed hairs to glabrous. *Leaves*: petiole 2–4 mm long, 1–2 mm diam; lamina elliptic to oblong-elliptic or narrowly so, 3–10(–12) by 1.5–4 cm (leaf index 1.5–3.5(–5)), coriaceous, not verruculose, shiny to dull, brown to dark greenish brown above, brown to greenish brown below, glabrous above, sparsely covered with appressed hairs below, base attenuate, apex rounded, emarginate, or acute, basal margins revolute, primary vein flat above, secondary veins distinct, 8–15 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins strongly raised above, reticulate. *Flowers* solitary in axils of leaves; flowering and fruiting pedicels 10–15 mm long, 1.5–2 mm diam, glabrous, articulated at c. 0.2 from the base, bracts 5–7, soon falling, the upper one c. 3 by 1.5 mm fide Mello-Silva & Pirani; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–4 by 3–5 mm, reflexed, outer side densely covered with appressed hairs; petals pale green in vivo, elliptic, 8–15 by 5–10 mm, outer side densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 10–15, green, maturing purple to red in vivo, black in sicco, ellipsoid, 7–10 by 3.5–5 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 1–7 by 0.5–1 mm. *Seed* ellipsoid, 8–9 by 4–5 mm, pale brown, smooth to slightly pitted, raphe not distinct from rest of seed.

Distribution — Brazil (Minas Gerais, S part of Espinhaço range).

Habitat & Ecology — In open campo rupestre vegetation or in gallery forest, on sandstone rocks. At elevations of 900–1250 m. Flowering: throughout the year; fruiting: February, April, September, October.

Vernacular names — Not recorded.

Note — *Guatteria rupestris* shares many features with the cerrado inhabiting *G. rigida*. For the differences with *G. rigida* see under that species.

142. *Guatteria sabuletorum* R.E.Fr. — Map 30

Guatteria sabuletorum R.E.Fr. (1939) 409, t. 27. — Type: *Ducke RB 19617* (holo S; iso RB), Brazil, Pará, Campina do Infiry, near Lago de Faro, 25 Jan. 1927.

Shrub or tree 6–12 m tall, c. 10 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2–7 mm long, 1–2 mm diam; lamina narrowly oblong to narrowly oblong-ovate, 10–23 by 4–8 cm (leaf index 3–3.7), chartaceous, not verruculose, shiny, greyish brown to dark brown above, brown below, glabrous above, sparsely covered with small appressed hairs to glabrous below, base obtuse to truncate, somewhat oblique or not, apex acute to acuminate (acumen to c. 15 mm long), primary vein impressed above, secondary veins distinct, 15–25 on either side of primary vein, flat to slightly raised above, smallest distance between loops and margin 3–7 mm, tertiary veins flat to slightly raised above, reticulate to percurrent. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 8–13 mm long, 1–1.5 mm diam, fruiting pedicels to c. 2 mm diam, sparsely covered with appressed hairs, articulated at c. 0.3 from the base, bracts 5–7, soon falling, the basal ones not seen, one upper bract seen, elliptic, c. 7 mm long; flower buds not seen; sepals free, broadly ovate-triangular, 3–5 by 3–5 mm, soon reflexed, outer side densely covered with appressed hairs; petals brownish green or greenish in vivo, elliptic to obovate or narrowly so, 10–16 by 4–8 mm, outer side densely covered with appressed and erect hairs; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* 20–30, colour in vivo not recorded, brown in sicco, ellipsoid to broadly ellipsoid, 7–10 by 5–7 mm, sparsely covered with appressed hairs, apex rounded to apiculate (apiculum < 0.5 mm long), wall 0.3–0.5 mm thick, stipes 4–5 by c. 1 mm. *Seed* ellipsoid, 8–9 by 5–6 mm, brown to dark brown, pitted, raphe raised.

Distribution — Amazonian Brazil (Pará).

Habitat & Ecology — In savanna ('campina') or non-inundated ('terra firme') forest, the type collection on dry sandy places ('in sabulosis siccis'). At elevations of about sea level. Flowering: January, June; fruiting: June.

Vernacular names — Not recorded.

Note — *Guatteria sabuletorum* is characterized by a truncate and somewhat oblique leaf base, loops far removed from the leaf margin (3–7 mm) and short stipes of 4–5 mm long.

143. *Guatteria saffordiana* Pittier — Fig. 69, 70a; Map 31

Guatteria saffordiana Pittier (1927) 77; R.E.Fr. (1939) 404. — Type: *Pittier 11855* (holo VEN; iso B, G, K, M, NY, P, US), Venezuela, Aragua, Rancho Grande, road from Maracay to Ocumare de la Costa, 11 Aug. 1925.

Guatteria knoopiana Pittier (1927) 78. — Type: *Pittier 10435* (holo VEN; iso G, K, NY, P, US), Venezuela, Miranda, Parque Knoop, Los Teques, 20 Aug. 1922.

Guatteria eximia R.E.Fr. (1939) 404, syn. nov. — Type: *Pittier 13487* (holo US; iso F), Venezuela, Guarico, Los Corozos, Puerto La Cruz valley, 800 m, May 1934.

Guatteria longedecurrens R.E.Fr. (1960) 22, syn. nov. — Type: *Bernardi 2255* (holo NY; iso G 3 sheets, K, S), Venezuela, Mérida, Pueblos del Sur, 1600–2200 m, June 1955.

Tree 3–20 m tall, 10–25 cm diam; young twigs sparsely covered with appressed or rarely erect hairs, soon glabrous. *Leaves*: petiole 5–15 mm long, 2–3 mm diam; lamina narrowly elliptic, sometimes narrowly ovate, 12–30 by 4–11 cm (leaf index 2–3.2), chartaceous to coriaceous, not verruculose, dull, greyish green above, brown below, glabrous above, rarely covered with some appressed hairs along primary vein and

Fig. 70 a. *Guatteria saffordiana* Pittier. Fruits, note connate sepals. – b. *Guatteria slateri* Standl. Fruit. – c. *Guatteria synsepala* Maas & Westra. Fruit. – d. *Guatteria tacarcunae* Maas & Erkens. Fruit. – e. *Guatteria ucayalina* Huber. Detail of leaf venation, lower side. – f. *Guatteria vallensis* Maas & Westra. Loose flower from below and above. – g. *Guatteria venezuelana* R.E.Fr. Flowers. – h, i. *Guatteria verruculosa* R.E.Fr. h. Flower and young fruits; i. fruit (a: *Riina et al. 265*, U; b: *McPherson & Merello 8295*, U; c: *Betancur et al. 811*, isotype MO; d: *Gentry et al. 16953*, MO; e: *Hill 12959*, U; f: *Monsalve B.685*, isotype MO; g: *Van der Werff 3624*, U; h: *Fosberg 19126*, holotype S; i: *Fosberg 19126*, isotype US).

secondary veins, sparsely covered with appressed or rarely erect hairs below, base acute to obtuse, sometimes slightly attenuate, apex acuminate (acumen 5–20 mm long), primary vein impressed above, secondary veins distinct, 12–15 on either side of primary vein, flat to slightly raised above, smallest distance between loops and margin 2–4 mm, tertiary veins flat to slightly raised above, reticulate. *Flowers* in 1–2(–occasionally more)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 5–20(–30) mm long, 1–1.5 mm diam, fruiting pedicels 10–30(–40) mm long, 2–3 mm diam, sparsely to rather densely covered with appressed or erect hairs, articulated at (0.1–)0.2–0.6 from the base, bracts 6–7, soon falling, the basal ones 2–3 mm long, the upper ones 5–20 mm long; flower buds depressed ovoid; sepals basally connate, broadly ovate-triangular, 6–8 by 5–6 mm, reflexed, outer side densely to rather densely covered with appressed hairs; petals cream or pale yellow in vivo, elliptic, 10–25 by 5–10 mm, outer side densely covered with appressed hairs; stamens 1–1.5 mm long, connective shield glabrous to papillate. *Monocarps* 50–100, green, maturing purple-black in vivo, brown to black in sicco, ellipsoid, 7–11 by 5–7 mm, glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.2–0.5 mm thick, stipes 10–25 by c. 1 mm. *Seed* ellipsoid, 8–10 by 5–6 mm, pale to dark brown, pitted to rugulose, raphe raised.

Distribution — Northern Venezuela (Aragua, Carabobo, Mérida, Miranda, Táchira, Trujillo, Yaracuy).

Habitat & Ecology — Almost always in cloud forest. At elevations of (350–)500–1800 m. Flowering: November to May; fruiting: throughout the year.

Vernacular names — Venezuela: Maguaná (*Lopez-Palacios 1612*), Raspadero (*Ruiz-Terán 1447*).

Notes — *Guatteria saffordiana* is a species fairly common in the cloud forests along the coastal region of Venezuela. It does not show many distinguishing features, except for the sepals which are basally fused. They often do not fall off during fructification but stay on the fruiting pedicel as a loose ring.

Guatteria saffordiana closely resembles the allopatric species *G. glauca*, which occurs in Bolivia, Peru, Ecuador and W Amazonian Brazil (Acre). It differs, however, by its distinctly fused sepals, a feature uncommon in the genus (and only rarely seen in *G. glauca*) and by the secondary veins which are flat to slightly raised on the upper side of the lamina (vs impressed in *G. glauca*).

Guatteria longedecurrens is put into synonymy of this species as the only difference is found in the slightly attenuate leaf base, which is also sometimes encountered in 'normal' *G. saffordiana*.

144. *Guatteria sanctae-crucis* Maas & Westra — Map 31

Guatteria sanctae-crucis Maas & Westra (2010) 271, f. 9. — Type: *Nee 37331* (holo LPB; iso MO, NY, SC, U), Bolivia, Santa Cruz, Prov. Ichilo, Parque Nacional Amboro, along Río Saguayo, 1.5–3 km NE of entrance into first Andean foothills, 375 m, 21 Dec. 1988.

Guatteria cinnamomea D.R.Simpson (1975) 305, non Hook.f. & Thomson (1855). — Type: *Jenssen S. 133* (holo F 3 sheets; iso MAD, NY, US, USM), Peru, Huánuco, Prov. Pachitea, Distr. Honoria, road to Tournavista, 240 m, 8 June 1964.

Tree 8–40 m tall, to c. 50 cm diam; young twigs densely to sparsely covered with erect, more or less curly, brown hairs, soon glabrous. *Leaves*: petiole 3–7 mm long, 1–2 mm diam; lamina narrowly oblong-elliptic to narrowly elliptic, 15–35 by 2.5–8 cm (leaf index 3.6–6.3), chartaceous, not verruculose, dull, grey, greyish brown to greyish black above, pale brown below, glabrous or sparsely covered with erect, curly, brown hairs towards the base above, sparsely or rarely rather densely covered with appressed and erect, more or less curly, whitish hairs below, base acute, apex acute to acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 15–25 on either side of primary vein, slightly raised above, smallest distance between loops and margin 3–7 mm, tertiary veins flat to slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 15–30 mm long, 1.5–2 mm diam, fruiting pedicels 25–40 mm long, 3(–10) mm diam, densely to rather densely covered with appressed to erect, more or less curly, brown hairs, becoming glabrous, articulated at 0.3–0.6 from the base, bracts 5–8, soon falling, the uppermost bract (only one seen) elliptic, c. 7 mm long; flower buds broadly ovoid to ovoid, slightly pointed; sepals free, broadly ovate-triangular to ovate-triangular, 8–12 by 4–9 mm, spreading, but soon reflexed, outer side densely covered with appressed to erect, more or less curly, brown hairs; petals greyish red, reddish brown or brown in vivo, elliptic, oblong-elliptic to obovate, 10–25 by 6–15 mm, outer side densely covered with appressed and erect, brown hairs; stamens 1–1.5 mm long, connective shield papillate to glabrous. *Monocarps* 25–75, green, maturing purple-green, brown to black in vivo, black in sicco, ellipsoid, 10–15 by 4–6 mm, glabrous, apex apiculate (apiculum < 1 mm long), wall 0.1–0.2 mm thick, stipes 4–20 by 0.5–1 mm. *Seed* ellipsoid, 8–11 by 4–5 mm, shiny brown, pitted to rugulose, raphe not distinct from rest of seed.

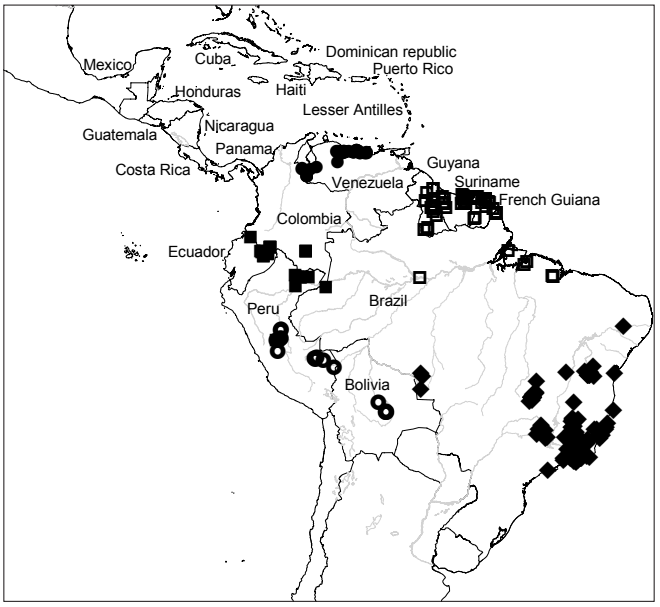
Distribution — Peru (Huánuco, Junín, Loreto, Madre de Dios, Pasco, Ucayali), Bolivia (Santa Cruz).

Habitat & Ecology — In tropical to subtropical, non-inundated or rarely periodically inundated forest. At elevations of 200–400(–1440) m. Flowering: January, February, April to July, September, December; fruiting: August, October, November.

Vernacular names — Peru: Carahuasca (*Jenssen S. 10*, *133*, *Tello 1734*), Carahuasca negra (*R. Oliveira 16*).

Notes — *Guatteria sanctae-crucis* can fairly easily be recognized by the relatively long and narrow leaves, the indument of erect, more or less curly hairs of its young leafy twigs, the large distance between loops of secondary veins and the leaf margin (3–7 mm) and also by the large sepals up to 12 mm long.

The indument varies much in density. A form with very dense indument was described as *G. cinnamomea* by Simpson (1975), referring to the pale brown or cinnamon colour of the indument on the young branchlets. Unfortunately, this aptly chosen name, being a later homonym, could not be maintained.



Map 31 Distribution of *Guatteria saffordiana* (●), *G. sanctae-crucis* (⭘), *G. scalarinervia* (■), *G. scandens* (□) and *G. sellowiana* (◆).

145. *Guatteria scalarinervia* D.R.Simpson — Map 31

Guatteria scalarinervia D.R.Simpson (1975) 306; Erkens et al. (2008) 507, f. 17, pl. 3; Maas & Westra (2011) 139. — 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 or rarely a ramiflorous tree 6–25 m tall, 5–25 cm diam; young twigs rather densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 15–25 mm long, 2–3 mm diam; lamina narrowly elliptic, 10–26 by 3.5–8 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, tertiary veins inconspicuous, flat to slightly raised above, reticulate. *Flowers* in up to many-flowered clusters on the trunk; pedicels 20–35 mm long, 1–1.5 mm diam, fruiting pedicels to c. 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 6–7, soon falling, basal bracts broadly ovate, c. 1 mm long, 2 uppermost bracts narrowly obtrullate to narrowly obovate-elliptic, 10–12 by 4–5 mm; flower buds broadly ovoid; sepals free, broadly ovate-triangular, 4–7 by 4–7 mm, appressed, outer side rather densely to densely covered with appressed hairs; petals green, maturing yellow or cream in vivo, ovate, elliptic, to oblong-obovate, 12–20 by 7–12 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 < 1 mm long), wall 0.1–1 mm thick, stipes 10–25 by c. 1 mm. *Seed* ellipsoid, 15–18 by 7–9 mm, dark brown, longitudinally and transversely grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Colombia (Caquetá), Ecuador (Carchi, Napo, Orellana, Sucumbíos), Peru (Loreto).

Habitat & Ecology — In non-inundated forest (one collection from periodically inundated tahuampa forest), on red, clayey to lateritic soil. At elevations of 200–1000 m. Flowering: April to June, August, October; fruiting: throughout the year.

Vernacular names — Colombia: Carguero (*Murillo A. & Román 588*). Ecuador: Dimonkawe (Huaorani name), Nagewe (Huaorani name) (*Naranjo & Freire 474*), Pungara-caspi (*Palacios & Neill 1120*), Pungaramuyo (*Palacios & Neill 1120*), Uñitawe (Huaorani name) (*Freire & Naranjo 481*).

Notes — *Guatteria scalarinervia* is the only cauliflorous tree species of the genus known to occur in Colombia, Ecuador and Peru so far. Moreover, it can be recognized by relatively long petioles and stipes.

Although this species has been treated as a member of sect. *Mecocarpus* (Maas et al. 2011), verruculae are not always evident in leaves on different collections, or are only clearly seen in part of the leaves in a specimen.

See also the note under *G. longicuspis*.

146. *Guatteria scandens* Ducke — Fig. 71; Plate 6c; Map 31

Guatteria scandens Ducke (1925) 10; R.E.Fr. (1939) 483. — Type: *Ducke RB 17874* (holo RB 2 sheets; iso B, S, U), Brazil, Pará, Belém, '10 May 1923 (flor.) and 10 Nov 1922 (fruct.)'.

Cauliflorous liana, climbing up to c. 20 m high, 2–4 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous, sometimes with some golden, appressed hairs. *Leaves*: petiole 6–13 mm long, 1–3 mm diam; lamina ovate to elliptic to narrowly so, 10–26(–33) cm long, 4–11 cm wide (leaf index 2.2–2.9), coriaceous, not verruculose, scabridulous, dull, greyish to greyish brown above, greenish to dark brown below, glabrous on both sides, base acute, sometimes slightly attenuate, obtuse, or rarely slightly cordate, apex acuminate (acumen 5–20 mm long), primary vein impressed above, secondary veins distinct, 5–12 on either side of primary vein, impressed above, smallest distance between loops and margin 3–6 mm, tertiary veins inconspicuous to conspicuous, raised above, reticulate. *Flowers* in compact clusters consisting of a varying number of (mostly) 1-flowered inflorescences on the trunk or also on leafless branchlets; pedicels 15–20 mm long, 1–1.5 mm diam, fruiting pedicels to c. 30 mm long, c. 2 mm diam, sparsely covered with appressed hairs, articulated at 0.2–0.4 from the base, bracts c. 6, soon falling, not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular to ovate-triangular, 4–6 mm long, c. 4 mm wide, appressed, outer side rather densely covered with appressed, brown hairs; petals greenish, maturing yellow in vivo, ovate, 10–40 mm long, 7–16 mm wide, outer base densely covered with appressed hairs, apex rather densely to densely so; stamens 1.5–2 mm long, connective shield hairy, convex to slightly umbonate. *Monocarps* 25–40, maturing dark red to purple-black or black in vivo, reddish brown, brown or black in sicco, ellipsoid, 13–17(–24) by 7–9(–13) mm, sparsely covered with appressed hairs, soon glabrous, apex rounded to apiculate (apiculum < 0.5 mm long), wall 0.1–0.4 mm thick, stipes 5–12 mm long, c. 1 mm diam. *Seed* ellipsoid, 11–16 by 6–7 mm, reddish black or black, rugose, longitudinally and transversely grooved, raphe not distinct from rest of seed.

Distribution — Guyana, Suriname, French Guiana, Amazonian Brazil (Amapá, Amazonas, Maranhão, Pará).

Habitat & Ecology — In non-inundated forest, on brown sand, also in swamp forest. At elevations of 0–350(–475) m. Flowering: April to June, October to January; fruiting: throughout the year.

Vernacular names — Brazil: Cipó-iuira, Cipó-ira (*Ducke RB 24162*), Cipó-uíra (*Ducke RB 17874*, *RB 24162*), Tata'y (the fire plant) (*Balée 793*). French Guiana: Kumataime/Mulokju (Wayana name), Malokopesi (Boni) (*Sauvain 109*), Mulokju (Wayana name) (*Veth 240*), Ndulu ndulu (Aluku name), Wime etni kamwi (Palikur name), Yoarno. Guyana: Karikahu, Kurihi koyoko. Suriname: Apukutitei (Sranang name), Bosolijf (Surinamese name), Kasalerodañ (Arawak name), Kasselerodang (Arawak name) (*Lanjouw & Lindeman 462*), Kiintongo (Aucan name) (*Van Andel et al. 4984*), Kirikahu (Arawak name), Kirikawa (Arawak name) (*Lanjouw & Lindeman 419*, *1285*), Kofiballi (Arawak name) (*BW 5569*), Krabita-tité (*BBS 13*), Krin tongo (Sranang name), Kufiballi (Arawak name), Kumataime, mulokju (Wayana name), Malakopesi (Boni name), Moelewa (Carib name) (*Lanjouw & Lindeman 1285*), Moerewa (Carib name) (*BW 1827*), Mulewa (Carib name), Mulokju (Wayana name), Ndulu ndulu (Boni), Olijf (Surinamese name) (*Lanjouw & Lindeman 1285*), Olijfrank (Surinamese name) (*BW 1808*), Olijfvrucht (Surinamese name) (*BW 1827*), Upupede (Trio name), Wanegu (Trio name).

Uses — French Guiana: Molokju: 'For smoking when the small fish mulok, that dwells in creeks, has given a disease that you do not want to eat it anymore'. 'Once he has seen people bathing with the bark in warm water' (*Veth & Manou 18*). Suriname: Bark used in Suriname by Trio Indians as a febrifuge (*BW 1827*). Kiin tongo: Eating the fruits will clean your tongue (*Van Andel et al. 4984*).

Note — *Guatteria scandens* is one of the very few species with a scandent habit in the genus *Guatteria*. The other lianescent species is *G. fractiflexa*, whereas in *G. beckii*, *G. flexilis*

and *G. synsepala* lianescent forms also have been observed, next to erect plants. It can also be recognized by its cauliflory and the scabridulous ('rough') leaves. The occurrence of lianas or plants of liana-like habit is rather exceptional in Neotropical *Annonaceae*, in contrast to the Old World where the percentage of climbing is much higher. Other Neotropical climbers are, e.g., *Annona haematantha* and *Annona scandens*.

147. *Guatteria schomburgkiana* Mart. — Plate 7d–f; Map 32

Guatteria schomburgkiana Mart. (1841) 38; R.E.Fr. (1939) 461, f. 22a, b. — *Cananga schomburgkiana* (Mart.) Baill. (1868a) 204. — *Guatteria guianensis* Klotzsch (1849) 1163, nom. nud. — *Guatteria vestita* Klotzsch (1849) 979, nom. nud. — *Guatteria vestita* Klotzsch var. *angustifolia* Klotzsch (1849) 979, nom. nud. — *Guatteria vestita* Klotzsch var. *latifolia* Klotzsch (1849) 979, nom. nud. — Type: *M.R. Schomburgk 993* (lecto B, selected by Scharf in Maas et al. 2011; isolecto B, BM, FI, G 3 sheets, NY, P), Guyana, without location.

Annona hostmannii Steud. (1843) 754. — Type: *Hostmann & Kappler 1221* (holo P; iso B, BM, C, F, G 3 sheets, K, MO, NY, P, S, U, US, W), Suriname, Para District. — *Guatteria schomburgkiana* Mart. var. *angustifolia* Klotzsch ex R.E.Fr. (1900) 17. — Type: *M.R. Schomburgk 1716* (holo B 2 sheets), Guyana, Comaka, Demerara River, Mar. 1848.

Guatteria schomburgkiana Mart. var. *latifolia* Klotzsch ex R.E.Fr. (1900) 17. — Type: *M.R. Schomburgk 1334* (holo B 4 sheets), Guyana, without location, Aug. 1843.

Guatteria sessilis R.E.Fr. (1900) 17, t. 2, f. 6–8. — Type: *Spruce 2661* (holo C; iso B, BR, F, G 2 sheets, K, NY, P, W), Brazil, Amazonas, Rio Uaupés, Ipanoré ('Panuré'), Oct. 1852.

Guatteria schomburgkiana Mart. var. *holosericea* R.E.Fr. (1938) 709. — Type: *Klug 2259* (holo S; iso F, G, K, MO, S), Peru, Loreto, Florida, Río Putumayo, near mouth of Río Zubineta, May–July 1931.

Guatteria sandwithii R.E.Fr. (1939) 466. — Type: *Sandwith 1578* (holo K 3 sheets; iso B, BM, F, G, NY, P, U, US), Guyana, Mazaruni Station, 3 Sept. 1937.

Guatteria spruceana R.E.Fr. (1939) 469, f. 23e. — Type: *Spruce 3698* (holo K; iso BR 2 sheets, P), Venezuela, Amazonas, San Carlos de Río Negro, Oct. 1854.

Guatteria flavovirens R.E.Fr. (1948b) 10, pl. 4b–d. Type: *Tamayo 3151* (holo US), Venezuela, Bolívar, Gran Sabana, Río Uarí, Mar. 1946.

Tree or shrub 2–30 m tall, 3–50 cm diam; young twigs densely covered with erect hairs, finally glabrous. *Leaves*: petiole 2–10 mm long, 1–2 mm diam; lamina narrowly elliptic, narrowly oblong-elliptic to narrowly ovate, 4–22 by 2–6 cm (leaf index 2.5–5), coriaceous, not verruculose, shiny or dull above, greyish, greyish black to dark brown above, pale brown to brown below, sparsely

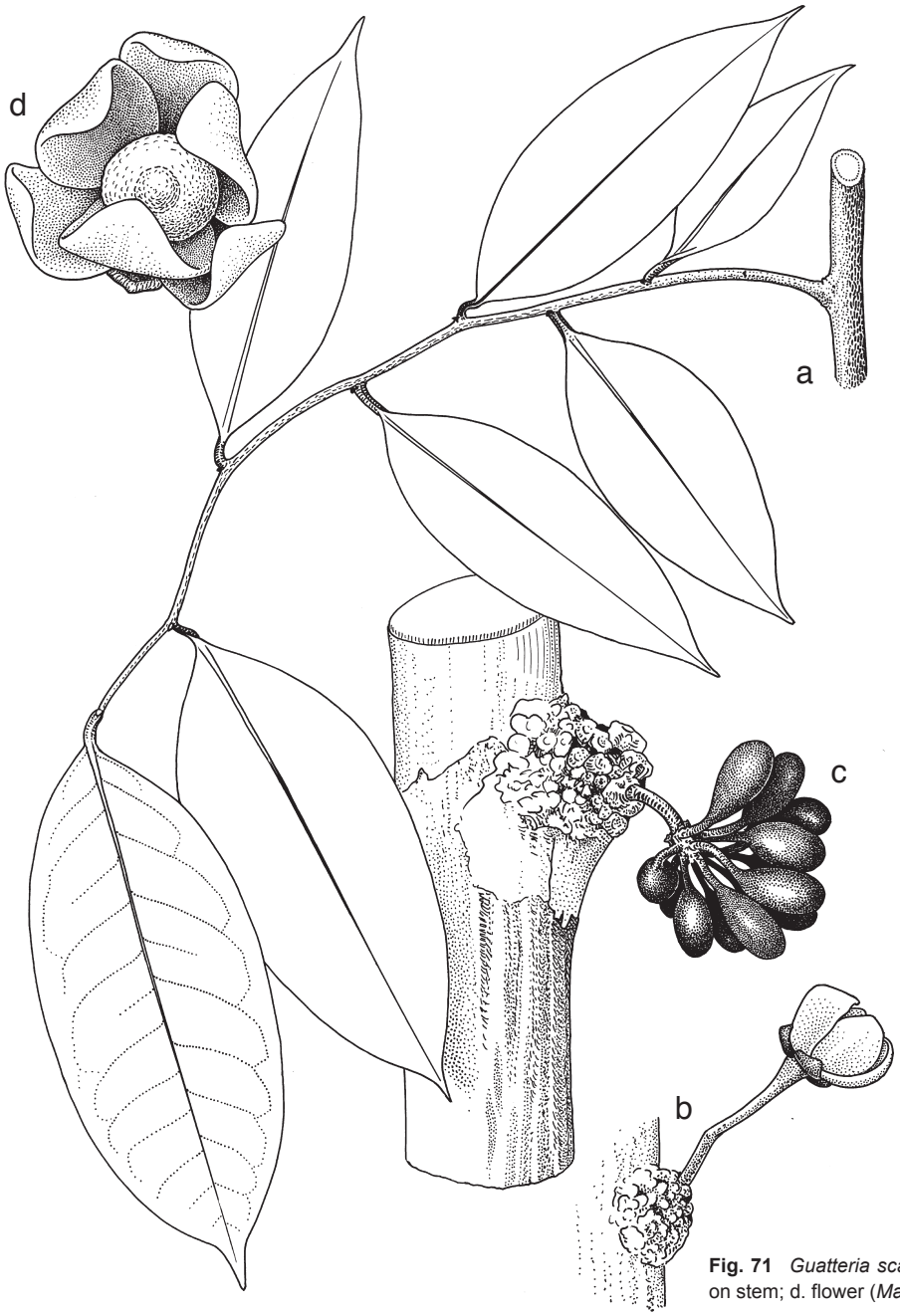


Fig. 71 *Guatteria scandens* Ducke. a. Branch; b. flower on stem; c. fruit on stem; d. flower (*Maas et al. 3600*, U). — Drawing by Hendrik Rypkema.

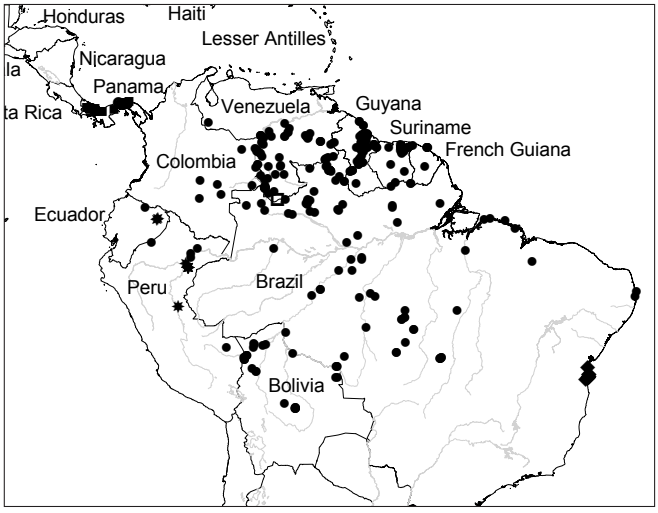
covered with appressed hairs when young, soon glabrous, densely covered with appressed or sometimes erect hairs below, base acute, obtuse, or attenuate, apex acuminate (acumen 5–25 mm long) to acute, primary vein impressed to flat above, secondary veins distinct, 8–13 on either side of primary vein, slightly raised to flat above, smallest distance between loops and margin 2–4 mm, tertiary veins slightly raised to flat above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves or on leafless branchlets; flowering pedicels 2–10 mm long, 1–2 mm diam, fruiting pedicels to c. 3 mm diam, densely to sparsely covered with more or less erect, pale brown hairs, becoming glabrous in fruit, articulated at 0.3–0.7 from the base, bracts 5–7, soon falling, basal bracts very broadly elliptic to circular, 2–3 mm long, upper one broadly elliptic, c. 5 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 2–5 by 2–5 mm, appressed, outer side densely covered with appressed hairs; petals green, yellow, or reddish in vivo, narrowly elliptic to oblong-elliptic, 10–30 by 4–8 mm, outer side densely to rather densely covered with appressed hairs; stamens c. 1 mm long, connective shield densely hairy. *Monocarps* 5–20, green, maturing black in vivo, brown to black in sicco, ellipsoid to globose, 6–13 by 5–8 mm, sparsely covered with appressed, brown hairs when very young, soon glabrous, apex rounded to apiculate (apiculum c. 0.5 mm long), wall 0.1–0.2 mm thick, stipes 0–3 mm long, c. 1 mm diam. *Seed* ellipsoid to broadly ellipsoid, or subglobose, 5–8 by 5–6 mm, brown to black, smooth, raphe slightly raised.

Distribution — Colombia (Guainía, Meta, Vaupés, Vichada), Venezuela (Amazonas, Bolívar, Tachira), Guyana, Suriname, French Guiana, Brazil (Amapá, Amazonas, Maranhão, Mato Grosso, Pará, Paraíba, Pernambuco, Rondônia, Roraima), Peru (Loreto), Bolivia (Beni, Pando, Santa Cruz).

Habitat & Ecology — In savanna-like vegetations (cerrado, campina, caatinga, campinarana), non-inundated, primary or secondary forest, or periodically inundated forest, often on white sandy soil. At elevations of 0–1000 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Brazil: Embira-vermelha (*O.T. Moura 67*), Envira-preta (*Milliken 816*), Imbira (*M.A. Sousa et al. 1046*), Invira (*Krukoff 6837*, *J.M. Pires 51684*). French Guiana: Mamayawé (Creole name). Guyana: Arara (*Tutin 58*), Arara, small kind (*Tutin 31*), Black maho (*Van Andel et al. 2312*), Black Yarri-Yarri (*Van Andel et al. 2268*), Smooth skin arara (*Raes et al. 38*). Suriname: Araraballi (Arawak name), Aremenango (Carib name), Aremenango wéwé (Carib name), Baakakungè (Saramaccan name), Boszuurzak (Surinamese name), Busisunsaka (Sranang name), Jane-jane (*LBB 13272*), Krukurutitei (Sranang name), Kurihi koyoko (Arawak name), Koelihi koejeko firiberoe (Arawak name), (*Stahel*, *Woodherbarium Suriname 254*), Kurihi koyoko karau bandikoro (Arawak name), Kwingé (Saramaccan name), Mayoballi wadilikoro (Arawak name), Panta (*Lindeman 5795*, *5892*), Payuriran (Carib name), Payurirang (Carib name), Pegrekoe (Sranang name) (*LBB 11211*), Pegrekoe-pisie (Sranang name) (*LBB 12126*), Peka (Saramaccan name), Pêpëêëpe uwii (Saramaccan name), Pêpëkusátu (Saramaccan name), Pepe wiri (Sranang name) (*Van Andel & Waterberg 5622*), Peprewiwiri (Sranang name), Savannepedreku (Sranang name), (*LBB 9817*, *11073*), Yaroyaro (Carib name). Venezuela: Anoncillo (*Aymard 6035*), Majagua anon (*Liesner 6071*), Majagua blanca (*Ll. Williams 14554*), Majagua negra (*Aymard 8994*), Majagua negra de altura (*Ll. Williams 14645*), Majagua verde (*Velazco 629*, *1427*), Majagüillo (*Breteler 4691*).

Notes — *Guatteria schomburgkiana* together with *G. citriodora*, *G. duckeana* and *G. stipitata* forms part of the *G. schomburgkiana* complex, see Table 4 (p. 59). This group, placed by Fries (1939) in sect. *Cephalocarpus* which originally consisted



Map 32 Distribution of *Guatteria schomburgkiana* (●), *G. sessilicarpa* (⭘), *G. slateri* (■), *G. spectabilis* (✷), *G. stenocarpa* (◆) and *G. stenopetala* (□).

of eight species, has as its main features short-pedicelled flowers and sessile to very shortly stipitate monocarps. The densely hairy connective shield also is a distinctive feature of this group (vs papillate or glabrous in most *Guatteria* species).

Guatteria schomburgkiana is widely distributed throughout tropical South America, and, in contrast to the other three species, is often found in savanna-like vegetations on white sandy soils. It differs from the other three species by an indument of appressed hairs on the lower side of the lamina. Most hairs are colourless, but a few hairs with brown cell content (as in the closely related *G. citriodora*) may be spotted among the other hairs. The leaf base mainly varies from acute to obtuse, but attenuate bases are also met with (mainly in Bolivian material).

Chanderbali & Gopaul 46 (WAG) from Guyana doubtfully belongs here as it is aberrant in having very narrow and elongate, almost linear petals of 15–25 by 3–4 mm and also by the erect, very short hairs. However, the hairy connective shield perfectly matchers that of *G. schomburgkiana*.

Contrary to what is normally seen in this species, a number of gatherings of *G. schomburgkiana* have erect rather than appressed hairs on the lower leaf side, or at least so on the primary vein. This is the case, among others, with populations in the Brazilian state of Paraíba. Otherwise these specimens match well with the species in general. This should merit further investigation.

148. *Guatteria scytophylla* Diels — Fig. 72; Map 33

Guatteria scytophylla Diels (1905) 127; R.E.Fr. (1939) 451, f. 20c, d. — Type: *Ule 5429* (holo B; iso BM, G, K, L), Brazil, Amazonas, Manaus, Mar. 1901.

Guatteria hyposericea Diels (1931) 76; R.E.Fr. (1939) 450. — Type: *Ll. Williams 4129* (holo F not seen; iso BM), Peru, Loreto, Lower Río Huallaga, 155–210 m, Oct.–Nov. 1929.

Guatteria krukoffii R.E.Fr. (1939) 442, f. 16c, d, syn. nov. — Type: *Krukoff 1487* (holo S; iso BM, F, G, K, MO, NY, S, U, US 2 sheets), Brazil, Rondônia, near Tabajara, Upper Jiparaná River (Upper Machado River region), Nov.–Dec. 1931.

Guatteria insignis R.E.Fr. (1939) 449. — Type: *Krukoff 8723* (holo NY; iso G, K 3 sheets, NY, U), Brazil, Mun. São Paulo de Olivença, Creek Belém, 26 Oct.–11 Dec. 1936.

Guatteria micans R.E.Fr. (1939) 451, f. 20b. — Type: *Ducke MG 7196* (holo S; iso RB), Brazil, Amazonas, Barcelos, 25 June 1905.

Tree 3–30 m tall, 4–60 cm diam; young twigs densely covered with a silky indument of appressed hairs ('sericeous'), soon glabrous. *Leaves*: petiole 5–25 mm long, 1–2 mm diam; lamina narrowly elliptic to ovate, rarely narrowly obovate, 8–25 by 6–11 cm (leaf index 2.3–4), chartaceous or rarely coriaceous,

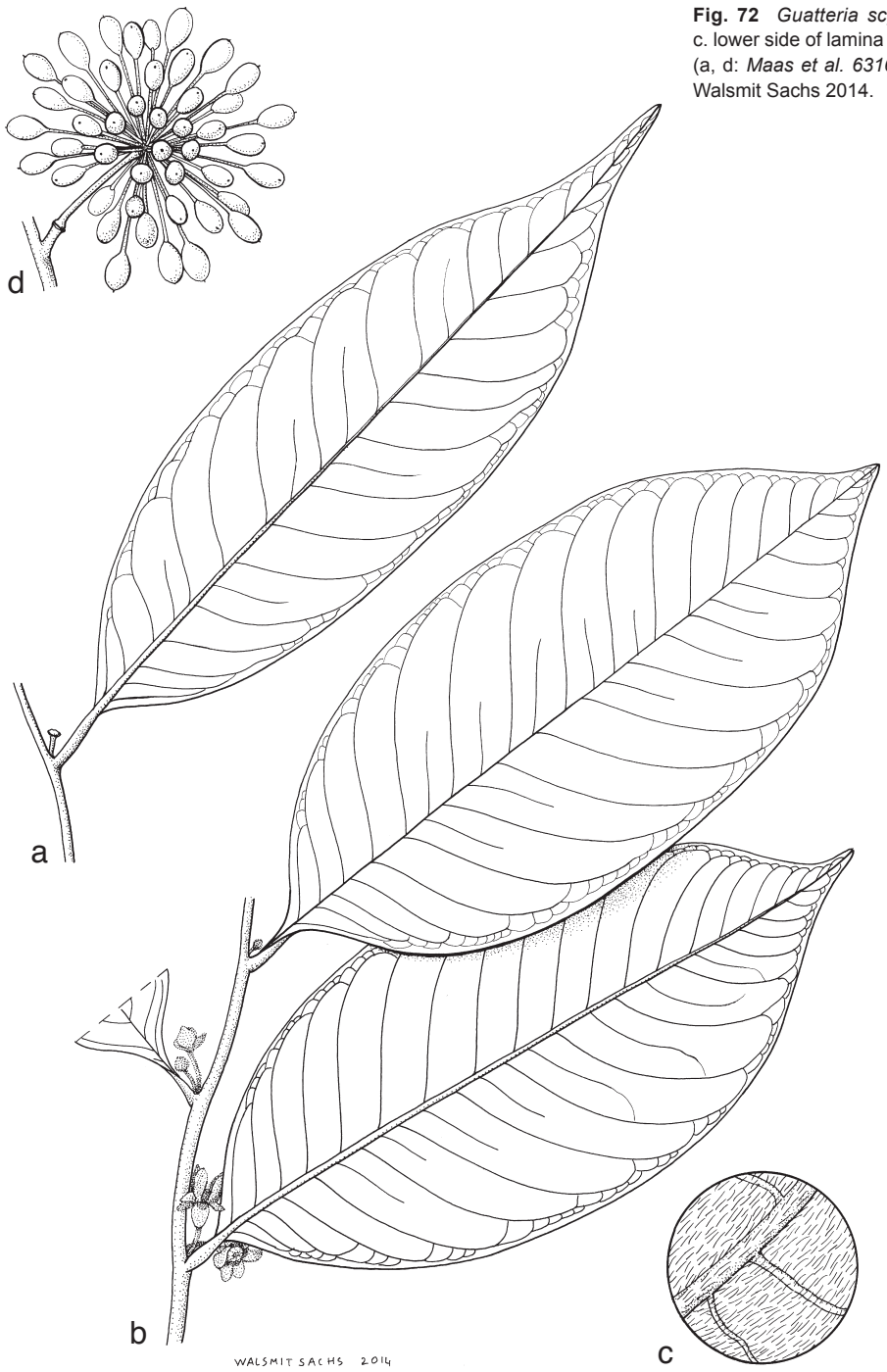


Fig. 72 *Guatteria scytophylla* Diels. a. One leaf; b. flowering branch; c. lower side of lamina showing dense indument of appressed hairs; d. fruit (a, d: *Maas et al. 6316*, U; b, c: *Cid et al. 9535*, U). — Drawing by Anita Walsmit Sachs 2014.

not verruculose, slightly shiny above, grey to greyish green, sometimes brownish above, brown to pale brown below, sparsely covered with appressed hairs, soon glabrous above, but primary vein often covered with erect, brown hairs, densely covered with appressed, greyish white hairs below, base acute to obtuse, extreme base attenuate, slightly decurrent along petiole, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins distinct, 12–20 on either side of primary vein, raised to slightly impressed above, smallest distance between loops and margin 2–4 mm, tertiary veins flat to slightly raised above, reticulate. *Flowers* in 1–3(–4)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–25 mm long, 1–2 mm diam, fruiting pedicels to c. 25 mm, c. 2 mm diam, densely to rather densely covered with appressed hairs, articulated at 0.2–0.5 from the base, bracts 5–6, soon falling, basal bracts broadly elliptic to elliptic, 1–2 mm long, upper ones 5–8 mm long; flower buds depressed ovoid, sometimes slightly pointed; sepals free, broadly ovate-triangular, 5–7 by 4–6 mm, initially appressed, but soon becoming spreading to reflexed, outer side densely covered with appressed hairs; petals green, greenish yellow, maturing cream or white in vivo, ovate to obovate, 10–25 by 5–12 mm, outer side densely covered with appressed hairs; stamens 1–1.5 mm long, connective shield papillate, umbonate. *Monocarps* 25–100, green, maturing red, black-purple to black in vivo, black or sometimes brownish in sicco, ellipsoid, 7–12 by 4–6 mm, sparsely covered with appressed hairs, soon glabrous, apex rounded to apiculate (apiculum 0.1–0.5(–1) mm long), wall 0.1–0.2 mm thick, stipes 10–30 by 0.5–1 mm. *Seed* ellipsoid, 7–9 by 5–6 mm, shiny brown, smooth to pitted and transversely grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Colombia (Caquetá, Vaupés, Vichada), Venezuela (Amazonas), Guyana, Peru (Huánuco, Junín, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Brazil (Acre, Amazonas, Mato Grosso, Pará, Rondônia), Bolivia (Beni, Pando, Santa Cruz).

Habitat & Ecology — In primary, non-inundated forest, sometimes in campinarana vegetation, often on sandy soil. At elevations of 0–1000(–1500) m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Bolivia: Ahuabaca (Chácobo name) (*Bergeron 910*, *Boom 4284*, *4444*), Peraquina negra (*Peña et al. 851*), Piraquina (*Meneces R. 2201*), Xahui (Chácobo name) (*Boom 4439*). Brazil: Envira (*J.C. Almeida INPA 4474*, *Krukoff 7940*), Envira-mole (*Rivero et al. 276*), Envira-preta (*Campbell et al. 8658*), Envireira (*Campbell et al. 8658*, *Medeiros & Oliveira 45*), Inviera (*Campbell et al. 8658*). Peru: Carahuasca (*T.D. Pennington et al. 17003*, *Rimachi Y. 923*, *Spichiger et al. 1771*), Carahuasco (*Croat 19794*), Espintana negra (*Grández & Sarmiento 340*), Panapualiki (Campa (Nomatsigenga) name) (*R.T. & J.C. Sčhuh 18*), Zorro caspi (*Daly et al. 5727*). Venezuela: Majagua verde (*Foldats & Velazco 9157*).

Uses — Colombia: Soft wood easy to cut and used in the construction of Baharaque houses ('Madera blanda para cortar y usada en la construcción de casa de bahareque') (*Cabrera R. 3737*).

Notes — *Guatteria scytophylla* is quite distinctive by the very densely sericeous and almost silvery lower leaf side, a feature not often seen in the genus *Guatteria*. This has also been nicely described by Diels (1931): 'Species pulchra indumento xylopioideo facile recognoscitur'. Another feature is encountered in the distinctly umbonate connective shield. After some hesitation we united in this species *G. hyposericea*, which differs from typical *G. scytophylla* (found in Central Amazonas, particularly near Manaus) in having narrower leaves with an acute leaf base, whereas the leaf base in *G. scytophylla* is mostly obtuse. Many transitions between both forms, however, convinced us that we had to join both species.

The seeds in this species are almost smooth with only very weak and shallow pits and grooves.

Cabrera R. 3737 (F) from the Colombian state of Caquetá doubtfully belongs here. It matches well with *G. scytophylla* in leaf shape and leaf indument, but the monocarps are larger on thicker stipes than normally seen in this species (monocarps 11–13 by 6 mm, stipes 1.5–2 mm diam). Moreover, the monocarps are densely covered with brown hairs, becoming glabrous only at maturity. The label reads: 'frutos ferruginosos y cuando maduros de color purpúreo'.

149. *Guatteria sellowiana* Schltdl. — Fig. 73; Plate 7g; Map 31

Guatteria sellowiana Schltdl. (1834) 323; R.E.Fr. (1939) 457, f. 21d–f. — *Cananga sellowiana* (Schltdl.) Warm. (1873) 144. — Type: *Sellow 1967 c 1479* (lecto B, selected by Fries 1939, 5 sheets; isolecto K), Brazil, Minas Gerais, Serra de Santo Antônio, 17 Oct. 1818.

Cananga sellowiana (Schltdl.) Warm. var. *montana* Warm. (1873) 145. — *Guatteria sellowiana* Schltdl. var. *montana* (Warm.) R.E.Fr. (1900) 14. — Type: *Warming s.n.* (holo C), Brazil, Minas Gerais, Caeté, Serra da Piedade, 4000–5000 ft, Feb. 18...

Guatteria australis A.St.-Hil. var. *pubens* Mart. (1841) 26. — *Guatteria pubens* (Mart.) R.E.Fr. (1939) 455. — Type: *Martius s.n.* (Obs. no. 47) (lecto M, here selected), Brazil, Rio de Janeiro, Petrópolis, ('M. Corcovado et ad Mandiocca'), Sept. 1817.

Guatteria mexiae R.E.Fr. (1939) 344. — Type: *Mexia 4249* (holo S; iso B, BM, F, G, K, NY, U, US), Brazil, Minas Gerais, Carangola ('Fazenda da Gramma, about 0.5 km North on trail'), 900 m, 27 Jan. 1930.

Guatteria umbrosa R.E.Fr. (1939) 455, t. 31. — Type: *Riedel s.n.* (holo S; iso LE, U), Brazil, Rio de Janeiro, Petrópolis ('Mandioca'), Oct. 1823.

Guatteria peckoltiana R.E.Fr. (1939) 457, f. 21c. — Type: *Peckolt 362* (holo BR 2 sheets), Brazil, Rio de Janeiro, Cantagalo ('Canta Gallo'), 1860.

Tree or shrub 2–25 m tall, 10–25 cm diam; young twigs densely to sparsely covered with erect, long-persisting hairs. *Leaves*: petiole 2–8 mm long, 1–2 mm diam; lamina narrowly elliptic to elliptic, 5–15 by 1.5–4 cm (leaf index 2.3–5.3), chartaceous, not verruculose, pale brown above, brown below, densely covered with erect hairs to glabrous above, densely covered with erect hairs below, base acute, apex acute, primary vein impressed above, secondary veins distinct, 10–14 on either side of primary vein, raised above, smallest distance between loops and margin c. 1 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; flowering and fruiting pedicels 5–25 mm long, 1–3 mm diam, fruiting pedicels rarely to c. 45 mm long, densely to sparsely covered with erect, brown hairs, articulated at 3–15(–20) mm from the base, bracts 3–5, soon falling, basal bracts broadly elliptic, 1.5–2 mm long, upper ones elliptic to elliptic-obovate, to c. 7 mm long; flower buds depressed ovoid; sepals free, broadly to shallowly ovate-triangular, 2–5 by 3–4 mm, reflexed, outer side densely covered with erect, curly, pale brown hairs; petals pale green in vivo, narrowly elliptic to elliptic, 6–20 by 4–10 mm, outer side densely covered with erect, curly, pale brown hairs to glabrous; stamens 1–1.5 mm long, connective shield hairy. *Monocarps* 15–40, blackish purple in vivo, black in sicco, ellipsoid, 5–8 by 4–5 mm, glabrous, apex apiculate (apiculum c. 0.5 mm long), wall c. 0.3 mm thick, stipes 5–10 by 1 mm. *Seed* ellipsoid, 5–8 by 4–5 mm, brown, pitted, raphe not distinct from rest of seed.

Map 33 Distribution of *Guatteria scytophylla* (●) and *G. talamancana* (✪).

Distribution — Brazil (Bahia, Distrito Federal, Espírito Santo, Goiás, Mato Grosso, Minas Gerais, Pernambuco, Rio de Janeiro, São Paulo).

Habitat & Ecology — In non-inundated, Atlantic rain forest or riparian forest in cerrado, often on brown, lateritic soil. At elevations of 0–1360 m. Flowering: March to May, September; fruiting: January to March, August to December.

Vernacular names — Not recorded.

Note — *Guatteria sellowiana* is characterized by young twigs and lower leaf sides which are densely covered with erect, brown and long-persisting hairs and by short pedicels. Among the species of the Atlantic Forest of Brazil, *G. sellowiana* stands out by its characteristic dense indument.

150. *Guatteria sessilicarpa* Maas & Setten — Plate 7h; Map 32

Guatteria sessilicarpa Maas & Setten (1988) 257, f. 13–15. — Type: *Mori & Kallunki 5037* (holo MO; iso U), Panama, Colón, Santa Rita Ridge Road, 17 km from Boyd-Roosevelt Highway, 450 m, 14 Mar. 1975.

Tree 5–20 m tall, 15–30 cm diam; young twigs rather densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 4–12 mm long, 3–4 mm diam; lamina narrowly elliptic to narrowly obovate, 18–33 by 5–10 cm (leaf index 3.3–3.6), coriaceous, rather densely verruculose, dull, grey to greyish brown above, brown below, glabrous above, except for some hairs

Fig. 73 *Guatteria sellowiana* Schltdl. Flowering and fruiting branch (*Harley et al. 26194*, U).

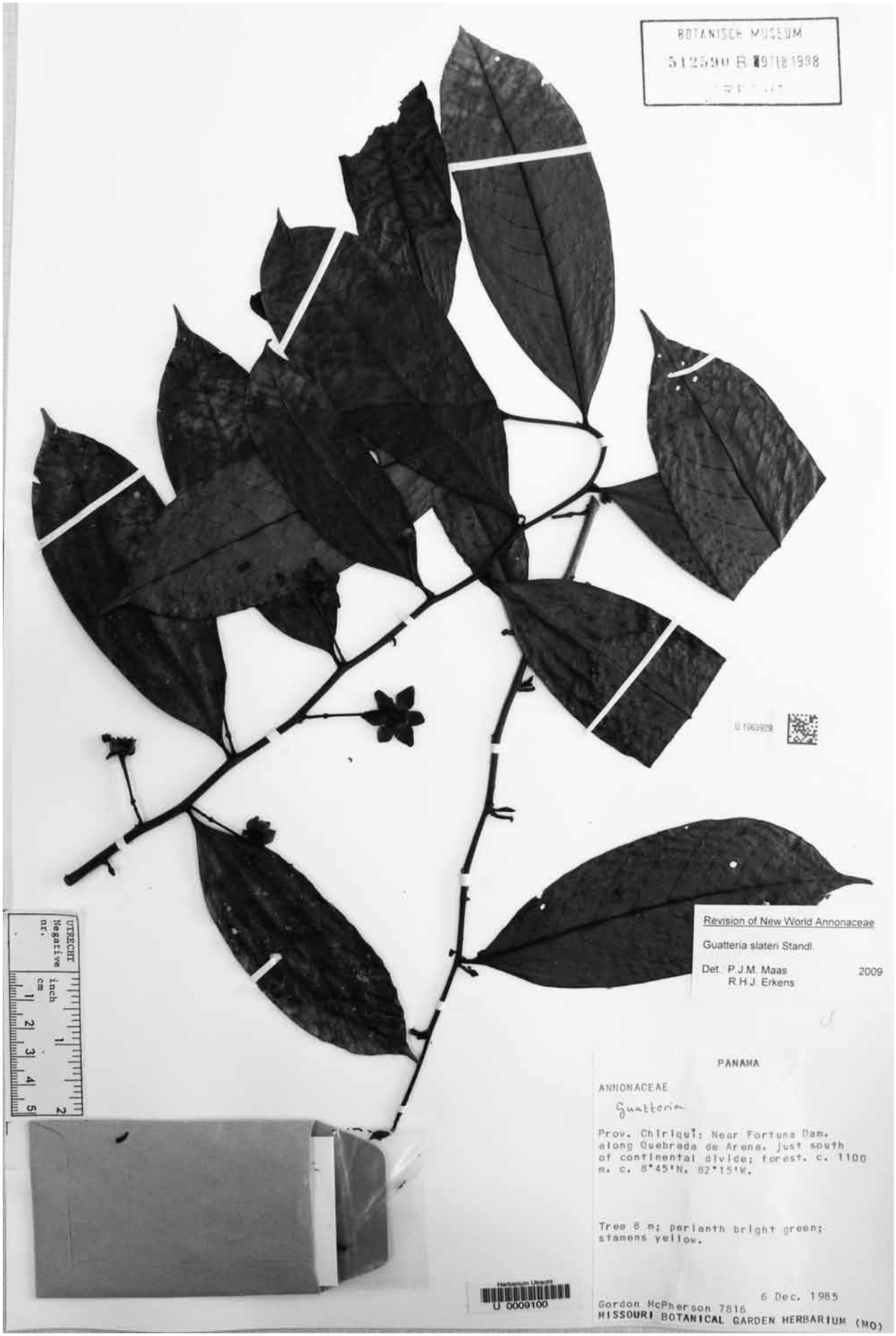


Fig. 74 *Guatteria slateri* Standl. Flowering branch (*McPherson 7816*, U).

at base and primary vein, and ciliate along basal margins, sparsely covered with appressed hairs to glabrous below, base acute, extreme base decurrent along petiole, basal margins often revolute, apex acuminate (acumen 5–10 mm long), primary vein impressed above, keeled below, secondary veins distinct, 17–20 on either side of primary vein, slightly raised above, smallest distance between loops and margin 5–10 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; flowering and fruiting pedicels 5–17 mm long, 2–3 mm diam, rather densely to sparsely covered with appressed hairs, articulated at 0.3–0.5 from the base, bracts 4–6, soon falling, only uppermost bracts seen, broadly elliptic, 6–7 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 7–9 by 8–10 mm, reflexed, outer side densely covered with appressed hairs; petals green, maturing yellow in vivo, elliptic, 11–20 by 7–13 mm, outer side densely covered with appressed hairs; stamens c. 2 mm long, connective shield papillate. *Monocarps* 4–20, green, maturing black in vivo, black in sicco, ellipsoid to ovoid, 12–23 by 8–14 mm, sparsely covered with appressed hairs, soon glabrous, apex rounded, wall 1–2 mm thick, stipes absent or up to 2 by 2 mm. *Seed* ellipsoid to ovoid, 12–15 by 5–8 mm, black, pitted and transversely grooved, raphe raised.

Distribution — Panama.

Habitat & Ecology — In forest. At elevations of 350–1000 m. Flowering: February, June, July; fruiting: March to June, August, November.

Vernacular name — Panama: Canalú (*Galdames et al. 3782*).

Note — *Guatteria sessilicarpa* is typical by its almost sessile monocarps, combined with coriaceous, rather densely verrucose leaves.

151. *Guatteria slateri* Standl. — Fig. 70b, 74; Map 32

Guatteria slateri Standl. (1929) 206; R.E.Fr. (1939) 517. — Type: *Cooper & Slater 177* (holo F; iso GH, NY), Panama, Chiriquí, Progreso, July–Aug. 1927.

Tree 4–30 m tall, to c. 30 cm diam; young twigs often zigzagging, rather densely covered with appressed, brown hairs, soon glabrous. *Leaves*: petiole 4–20 mm long, 1–3 mm diam, decurrent as slightly prominent ridges in young twigs; lamina narrowly elliptic to narrowly obovate, 7–24 by 2.5–8.5 cm (leaf index 2.7–3.2), chartaceous to coriaceous, not verruculose, dull, greyish green to dark brown above, brown below, glabrous above, sparsely covered with appressed, brown hairs to glabrous below, base acute to attenuate, apex acuminate (acumen 5–15 mm long), primary vein slightly raised to flat above, often keeled below, secondary veins distinct, 8–15(–20) on either side of primary vein, raised above, smallest distance between loops and margin 1–2 mm, tertiary veins raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; pedicels 15–32 mm long, 1–2 mm diam, fruiting pedicels up to c. 40 mm long, rather densely to sparsely covered with appressed hairs, articulated at c. 0.3 from the base, bracts 5–8, soon falling, basal bracts broadly to very broadly elliptic, 1.5–2.5 mm long, uppermost bracts obovate to elliptic, 7–8 mm long, occasionally the third bract from above foliaceous, 22–26 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–6 by 3–7 mm, apically reflexed or appressed, outer side sparsely covered with appressed hairs to glabrous; petals green, maturing yellow in vivo, ovate, obovate to rhombic, 8–16 by 5–11 mm, outer side sparsely to densely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate to hairy. *Monocarps* 20–60, green, maturing red to finally black in vivo, black in sicco, ellipsoid, 8–10{–13} by 5–8 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate, sometimes rounded (apiculum < 1 mm long), wall 0.1–0.2 mm thick, stipes 3–10 by 1–2 mm. *Seed* ellipsoid, 7–10 by 5–7 mm, dark brown, transversely grooved to pitted, raphe not distinct from rest of seed.

Distribution — Panama.

Habitat & Ecology — In primary wet forest or montane (elfin) forest. At elevations of (0–)600–2100 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular name — Panama: Malagueto prieto.

Notes — *Guatteria slateri* is a species mostly found at high elevations, although the type has been collected at sea level. It has many features in common with *G. costaricensis*, the main differences being the shorter stipes (3–6 vs 8–14 mm), longer petioles (4–20 vs 3–7 mm) and longer pedicels (15–32 vs 10–20 mm). Another difference is found in the upper leaf side, which is glabrous in *G. slateri*, whereas the primary vein is covered with hairs in *G. costaricensis*.

Ripe monocarps are rarely found in this species, except for *Maas et al. 9513*, with monocarps (measured from spirit material!) of 10–13 mm long, thus somewhat longer than cited in the description based on herbarium collections.

152. *Guatteria spectabilis* Diels — Fig. 75; Map 32

Guatteria spectabilis Diels (1924) 138; R.E.Fr. (1939) 533, f. 38a, b. — Type: *Tessmann 3235* (holo B; iso G, S), Peru, Loreto, Middle Río Ucayali, near Yarinacocha, 155 m, 3 Oct. 1923.

Tree 12–35 m tall, 15–50 cm diam; young twigs sparsely covered with appressed hairs, very soon glabrous. *Leaves*: petiole 5–18 mm long, 2–3 mm diam; lamina narrowly elliptic, 15–29 by 6–10 cm (leaf index 2.5–3.3), coriaceous, not verruculose, dull, grey to dark greyish brown above, brown below, glabrous above, sparsely covered with appressed hairs below, base attenuate, decurrent along the petiole to obtuse, apex acuminate (acumen c. 10 mm long), primary vein impressed above, strongly keeled below, secondary veins distinct, 15–20 on either side of primary vein, slightly raised above, smallest distance between loops and margin 3–4 mm, tertiary veins slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 15–50 mm long, 1–3{–5} mm diam, rather densely covered with appressed hairs to glabrous, articulated at 0.3–0.5 from the base, bracts 6–8, soon falling, the basal ones not seen, the 2 upper ones ovate-elliptic, to c. 6 mm long; flower buds broadly ovoid; sepals basally connate, triangular to deltate, 8–15 by 9–10 mm, strongly reflexed, margins revolute, outer side densely covered with appressed hairs; petals green in vivo when young, maturing creamy green to yellow, ovate-elliptic to broadly obovate, 25–30{–40} by 10–25 mm, outer side densely covered with erect and appressed, brown hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* and *seed* not seen.

Distribution — Amazonian Ecuador (Napo, Orellana), Peru (Loreto).

Habitat & Ecology — In periodically inundated (restinga) forest, flooded by a mixture of black and white water, or in primary non-inundated forest, with *Iryanthera hostmannii*, *Oenocarpus bataua*, *Iriartea deltoidea*, *Simarouba amara* (Ecuador), on red soil. At elevations of 110–260 m. Flowering: August, October, November; fruiting: unknown.

Vernacular name — Peru: Cararasca (*Tessmann 3235*).

Note — *Guatteria spectabilis* is highly characteristic by large, reflexed sepals (to 15 mm long!) with recurved margins and large petals up to 40 mm long.

Fig. 75 *Guatteria spectabilis* Diels. Flowering branch (*Maas et al. 8223*, U).

153. *Guatteria stenocarpa* Lobão, Maas & Mello-Silva — Map 32

Guatteria stenocarpa Lobão, Maas & Mello-Silva (2010) 122, f. 1G–I. — Type: *Jardim et al. 3096* (holo RB; iso CEPEC, MO, NY, SPF, U), Brazil, Bahia, Itacaré, Loteamento da Marambaia, viscinal que leva à fazenda, c. 1 km da Rodovia BA-001, 29 Oct. 2000.

Tree or shrub 5–8 m tall, diam not recorded; young twigs glabrous. *Leaves*: petiole 6–12 mm long, 2–4 mm diam; lamina narrowly obovate to narrowly elliptic, 11–22 by 4–8 cm (leaf index 2.2–3), subcoriaceous, not verruculose, shiny, brown to pale green above, pale brown below, glabrous above and below, base attenuate, apex acute, primary vein impressed above, secondary veins distinct, 18–21 on either side of primary vein, raised above, smallest distance between loops and margin 1–3 mm, tertiary veins inconspicuous, raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 15–35 mm long, c. 1 mm diam, fruiting pedicels 1–2 mm diam, glabrous, articulated at c. 0.3 from the base, bracts 6–7, soon falling, not seen; flower buds depessed ovoid; sepals free, broadly ovate-triangular, 2–6 by 3–6 mm, reflexed, outer side densely covered with erect, curly, brown hairs; petals cream or yellow in vivo, broadly ovate to elliptic, 6–24 by 6–15 mm, outer side densely covered with erect, curly, brown hairs; stamens c. 2 mm long, connective shield hairy. *Monocarps* 8–20, green in vivo, black in sicco, narrowly ellipsoid, 18–25 by 6–8 mm, glabrous, apex rounded, wall c. 1 mm thick, stipes 5–10 by 1 mm. *Seed* narrowly ellipsoid, c. 20 by 6 mm, dark brown, longitudinally and transversely grooved, raphe impressed.

Distribution — Brazil (Bahia).

Habitat & Ecology — In periodically inundated or non-inundated, Atlantic rain forest, often on brown, lateritic soil. At elevations of 0–100 m. Flowering: March to May, September; fruiting: January to March, August to December.

Vernacular names — Not recorded.

Note — *Guatteria stenocarpa* is similar to *G. pogonopus* and *G. oligocarpa* by the subcoriaceous and glabrous leaves. *Guatteria pogonopus* and *G. oligocarpa*, however, have smaller monocarps with a maximum length of 12 mm (vs > 20 mm in *G. stenocarpa*). The monocarps are narrowly ellipsoid, a characteristic only shared in SE Brazil with *G. capixabae.*

154. *Guatteria stenopetala* R.E.Fr. — Fig. 76; Map 32

Guatteria stenopetala R.E.Fr. (1957a) 329. — Type: *Maguire et al. 36970* (holo NY; iso F, S, US), Venezuela, Amazonas, Cerro de la Neblina, Río Yatua, just S of Camp 3, 650 m, 29 Dec. 1953.

Tree c. 8 m tall, diam not recorded; young twigs rather densely covered with erect and appressed, brown hairs, soon glabrous. *Leaves*: petiole 4–6 mm long, 1–2 mm diam; lamina elliptic to narrowly so, 5–11 by 3–5 cm (leaf index 2–2.6), coriaceous, not verruculose, shiny, dark brown to brown above, brown below, sparsely covered with appressed hairs to almost glabrous above, sparsely covered with appressed hairs below, base acute to obtuse, apex acuminate (acumen 5–10 mm long), primary vein flat to slightly raised above, secondary veins distinct, 5–10 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 30–40 mm long, c. 0.5 mm diam, fruiting pedicels to c. 1 mm diam, rather densely to sparsely covered with erect and appressed hairs to almost glabrous, articulated at c. 0.3 from the base, bracts 5–6, soon falling, occasionally a small, foliaceous bract halfway between base and articulation, elliptic, 7–8 mm long on tiny petiole c. 1 mm long, no other bracts seen; flower buds ovoid; sepals free, broadly ovate-triangular, 3–4 by 3–4 mm, apex reflexed, outer side densely covered with appressed, brown hairs; petals green, narrowly oblong to narrowly elliptic, 7–12 by 3–4 mm, outer side densely covered with appressed, brown hairs; stamens c. 1 mm long, connective shield hairy. *Monocarps* 10–25, green in vivo, black in sicco, ellipsoid, 9–10 by 4–5 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 13–17 by c. 1 mm. *Seed* ellipsoid, 8–9 by 4–5 mm, shiny brown, pitted to transversely grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Venezuela (Amazonas).

Habitat & Ecology — In Clusia 'moss-forest'. At an elevation of c. 650 m. Flowering: December; fruiting: December.

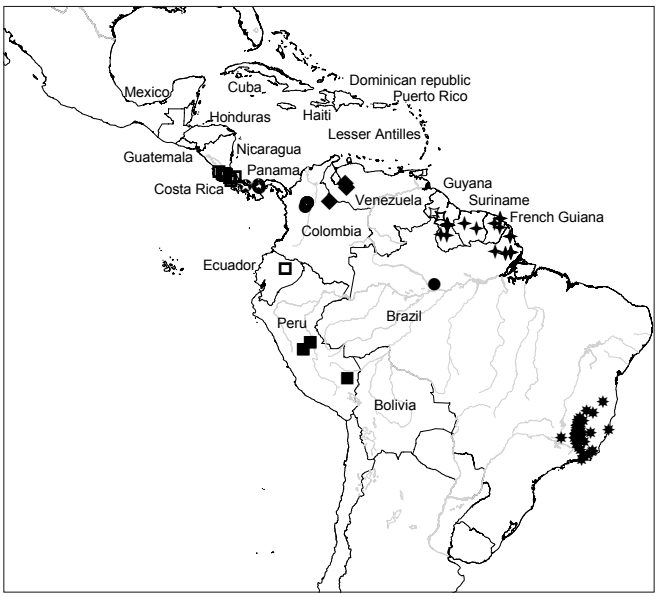
Vernacular names — Not recorded.

Note — *Guatteria stenopetala*, only known from the type collection, is quite remarkable by its very tiny flowers with petals less than 15 mm long and sepals up to 4 mm long. Other features of this species are the small, coriaceous leaves and the long-stalked flowers with pedicels up to c. 40 mm long. For differences with *G. trichostemon* see under the latter.

155. *Guatteria stenophylla* Maas & Westra, *sp. nov.* — Fig. 77; Map 34

Species foliis angustissimis apice longe acutis vel acuminatis foliis Xylopiae simulantibus et petalis parvis distincta. — Typus: *Mori & Gracie 21842* (holo U; iso INPA, NY), Brazil, Amazonas, Rio Cuieiras, Campina de Jaradá, 23 July 1991.

Tree c. 3 m tall, diam not recorded; young twigs rather densely covered with erect, brown hairs to c. 1 mm long, soon glabrous. *Leaves*: petiole 5–8 mm long, 0.5–1 mm diam; lamina narrowly ovate, 7–11 by 1.5–2.5 cm (leaf index 4.6–5.3), chartaceous, not verruculose, dull, dark brown above, brown below, glabrous above, sparsely covered with some scattered appressed hairs along the primary vein to glabrous below, base acute to obtuse, apex long-acute to acuminate (acumen 10–20 mm long), primary vein flat above, secondary veins distinct, 12–15 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 10–19 mm long, 0.5–1 mm diam, rather densely covered with erect, brown hairs to c. 2 mm long, articulated at c. 0.3 from the base, bracts 5–6, soon falling or sometimes present to almost



Map 34 Distribution of *Guatteria stenophylla* (●), *G. synsepala* (⭘), *G. terminalis* (■), *G. verrucosa* (□), *G. verruculosa* (◆), *G. villosissima* (✳), *G. wachenheimii* (✦), *G. wokomungensis* (⌑) and *G. zamorae* (✪).

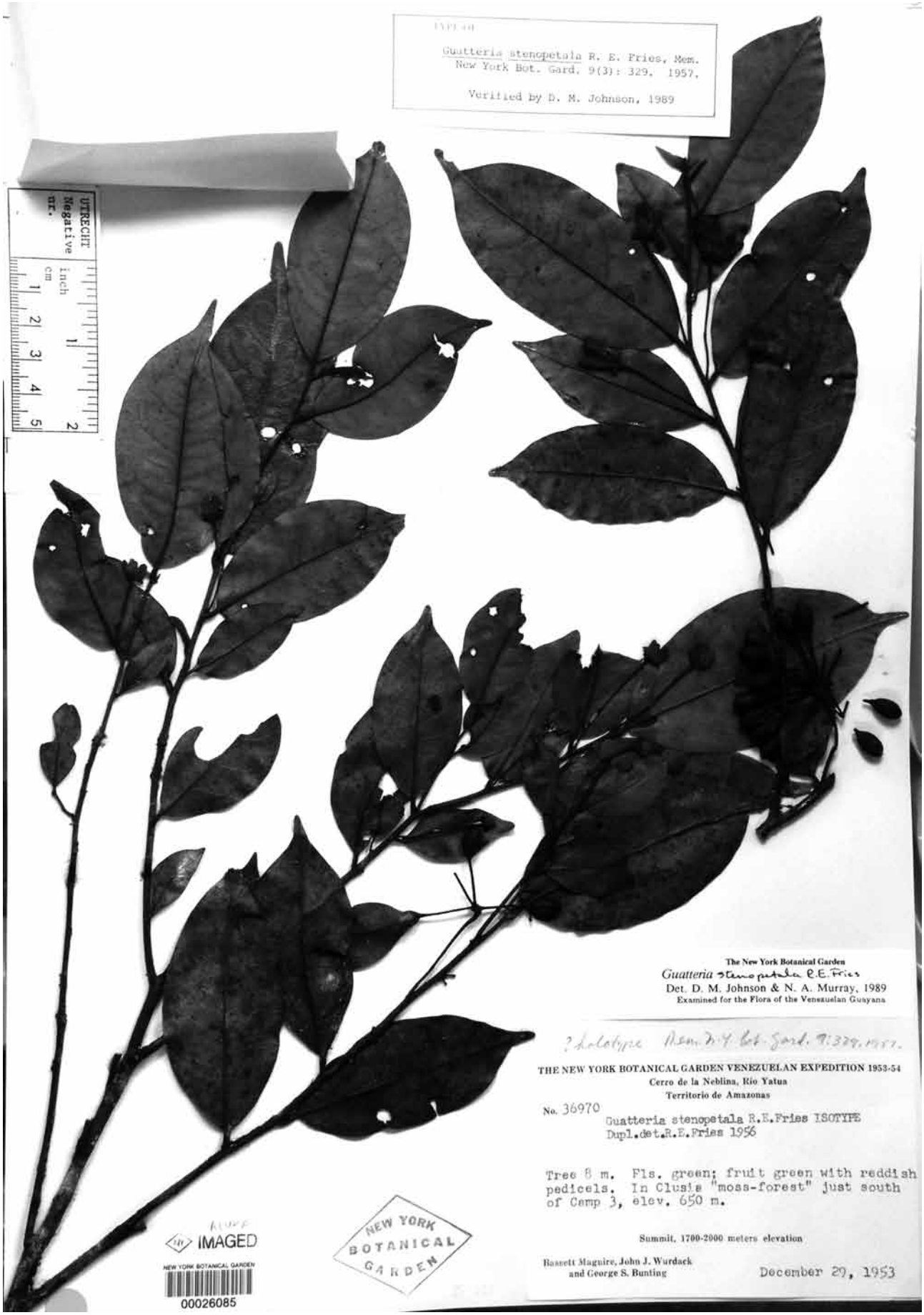


Fig. 76 *Guatteria stenopetala* R.E.Fr. Flowering branch (*Maguire et al. 36970*, holotype NY).

Fig. 77 *Guatteria stenophylla* Maas & Westra. Flowering branch (*Mori & Gracie 21842*, holotype U).

Fig. 78 *Guatteria stipitata* R.E.Fr. Fruiting branch (*Maguire et al. 41586*, U).

flowering stage, the upper ones narrowly ovate-elliptic, to c. 5 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–5 by 3–5 mm, margins reflexed, outer side rather densely covered with appressed to erect, brown hairs to c. 2 mm long; petals green in vivo, elliptic to ovate, 7–11 by 3–5 mm, outer side densely covered with appressed, brown hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* and *seed* not seen.

Distribution — Amazonian Brazil (Amazonas).

Habitat & Ecology — In campina vegetation. At an elevation of c. 50 m. Flowering: July; fruiting: unknown.

Vernacular names — Not recorded.

Notes — *Guatteria stenophylla*, one of the few savanna inhabiting species of the genus, can at first glance be recognized by very narrow and long-tipped leaves and very small petals (up to 11 mm long).

Carvalho, *Webber et al. 146* (HUAM, U), collected on 25 October 1988 in a sandy campinarana at UHE Balbina, Estrada Cachoeira Morena, Amazonas, Brazil may belong here. This fruiting specimen has the following features:
Shrub, c. 2.8 m tall; flowers green; fruiting pedicels c. 15 mm long, 1 mm diam. *Monocarps* c. 25, green in vivo, black in sicco, ellipsoid, 6–9 by 3–4 mm, glabrous, apex distinctly apiculate (apiculum c. 0.5 mm long), wall 0.1–0.2 mm thick, stipes c. 1 by 1 mm. *Seed* ellipsoid, 6–8 by 3–4 mm, dark brown, deeply pitted.

156. *Guatteria stipitata* R.E.Fr. — Fig. 78; Plate 8a; Map 35

Guatteria stipitata R.E.Fr. (1939) 465; Murillo A. & Restrepo (2000) 114, f. 34. — Type: *Krukoff 6907* (holo S; iso C, F, G 2 sheets, LE, MO, NY, RB 2 sheets, S, SPF, U, US), Brazil, Amazonas, Basin of Rio Madeira, Mun. Humaitá, near Livramento on Rio Livramento, 12 Oct.–6 Nov. 1934.

Tree 5–35 m tall, 10–30 cm diam; young twigs densely covered with erect, brown, long-persistent hairs. *Leaves*: petiole 5–10 mm long, 1–4 mm diam; lamina narrowly oblong-elliptic to narrowly ovate, 10–37 by 4–15 cm (leaf index 2.3–3.8), coriaceous, not verruculose, dull, greyish to greyish black above, brown below, rather densely covered with erect, brown hairs but soon almost glabrous above, densely covered with erect, brown hairs below, hairs simple or in bundles of 2–4, base acute to obtuse, basal margins mostly revolute, apex acuminate (acumen 5–20 mm long), primary vein impressed above, secondary veins distinct, 10–20 on either side of primary vein, raised above, smallest distance between loops and margin 3–6 mm, tertiary veins raised above, reticulate. *Flowers* in 1–3(–4)-flowered inflorescences in axils of leaves or sometimes on leafless branchlets; pedicels 5–10 mm long, 1.5–2 mm diam, fruiting pedicels 5–22 mm long, 2–4 mm diam, densely covered with erect, brown hairs, articulated at 0.4–0.7 from the base, bracts 5–7, soon falling, not seen; flower buds broadly ovoid; sepals free, ovate-triangular to broadly ovate-triangular, 3–6 by 4 mm, soon reflexed, outer side densely covered with erect, brown hairs; petals green, maturing cream or red in vivo, narrowly elliptic to elliptic, 12–20 by 4–9 mm, outer side densely covered with erect, brown hairs; stamens 1–1.5 mm long, connective shield densely hairy. *Monocarps* 5–20, green, maturing purplish black in vivo, black, sometimes brown in sicco, ellipsoid, 8–16 by 5–11 mm, densely covered with erect, brown and sometimes also with appressed hairs, soon glabrous, apex rounded to apiculate (apiculum < 0.5 mm long), wall 0.3–0.6 mm thick, stipes (3–)5–11 by 1–2 mm. *Seed* ellipsoid, 7–12 by 5–7 mm, brown, smooth, raphe not distinct from rest of seed.

Distribution — Colombia (Amazonas, Antioquia, Caquetá, Meta, Santander), Venezuela (Amazonas), Ecuador (Morona-Santiago, Napo, Orellana), Peru (Amazonas, Loreto, Pasco, San Martín).

Habitat & Ecology — In primary, non-inundated rain forest, on white sandy to red, clayey soil. At elevations of 100–1200 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Colombia: Dujeko (Yucuna name) (*Vester & Matapi 170*), Jigomada (Huitoto name) (*Vester & Castro 147*), Jïrïda (Huitoto name) (*Vester et al. 327*), Nagui (*García-Barriga 18210*). Ecuador: Oñintahua (*Gudiño et al. 939*), Yais (Shuar name) (*Neill et al. 15437*). Peru: Carahuasca (*Neill et al. 10368*), Cara huasca (*Daly et al. 5752*), Chinanim (*C. Díaz et al. 6995*), Yumi yeis (*Huashikat 1433*).

Notes — *Guatteria stipitata* together with *G. citriodora*, *G. duckeana* and *G. schomburgkiana* forms part of the *G. schomburgkiana* complex, see Table 4 (p. 59). This group, placed by Fries (1939) in sect. *Cephalocarpus*, which originally consisted of eight species, has as its main features short-pedicelled flowers and in general sessile to very shortly stipitate monocarps. The densely hairy connective shield is also a distinctive feature of this group (vs papillate or glabrous in most *Guatteria* species).

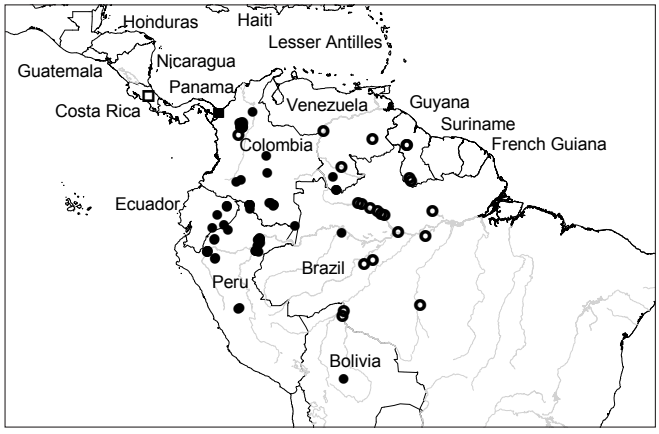
Guatteria stipitata, when in fruit, can easily be distinguished from *G. citriodora* and *G. schomburgkiana* by distinctly stipitate monocarps, the stipes 5–11 mm long and often longer than the monocarp body. The other species are characterized by sessile to subsessile monocarps, the stipe, when obvious, always shorter than the monocarp body. Non-fruiting specimens of *G. stipitata* can be much harder to tell apart from *G. citriodora*. The best way is to examine the leaves: in *G. stipitata* the basal leaf margins are mostly revolute whereas leaf margins in *G. citriodora* generally are not or only weakly revolute. Furthermore the indument on the lower leaf side in *G. stipitata* commonly consists of somewhat coarser hairs, equally with brown cell content, and there are quite many 2–4(–more)-bundled hairs, particularly near the primary vein.

According to various labels the colour of the petals is red, a colour rarely encountered in the genus *Guatteria*.

In the Flora of the Jenaro Herrera Arboretum (Spichiger et al. 1989) this species has been incorrectly identified as *G. citriodora*.

Two specimens from the Brazilian state of Acre, in the neighbourhood of Cruzeiro do Sul, *Cid et al. 10477* (U) and *10708* (U), may well belong here but as fruits are lacking the identification is not certain.

Two collections from the Colombian department of Antioquia, *Callejas et al. 8734* and *8784*, probably represent the northern limit of this species. They match *G. stipitata* well except for the indument consisting of a sparse cover of appressed hairs instead of the often dense cover of erect hairs in average *G. stipitata*. A third collection from Antioquia, *Callejas et al. 8858*, has the typical indument of erect hairs, though.



Map 35 Distribution of *Guatteria stipitata* (●), *G. subsessilis* (⭘), *G. tacarcunae* (■) and *G. tenera* (□).

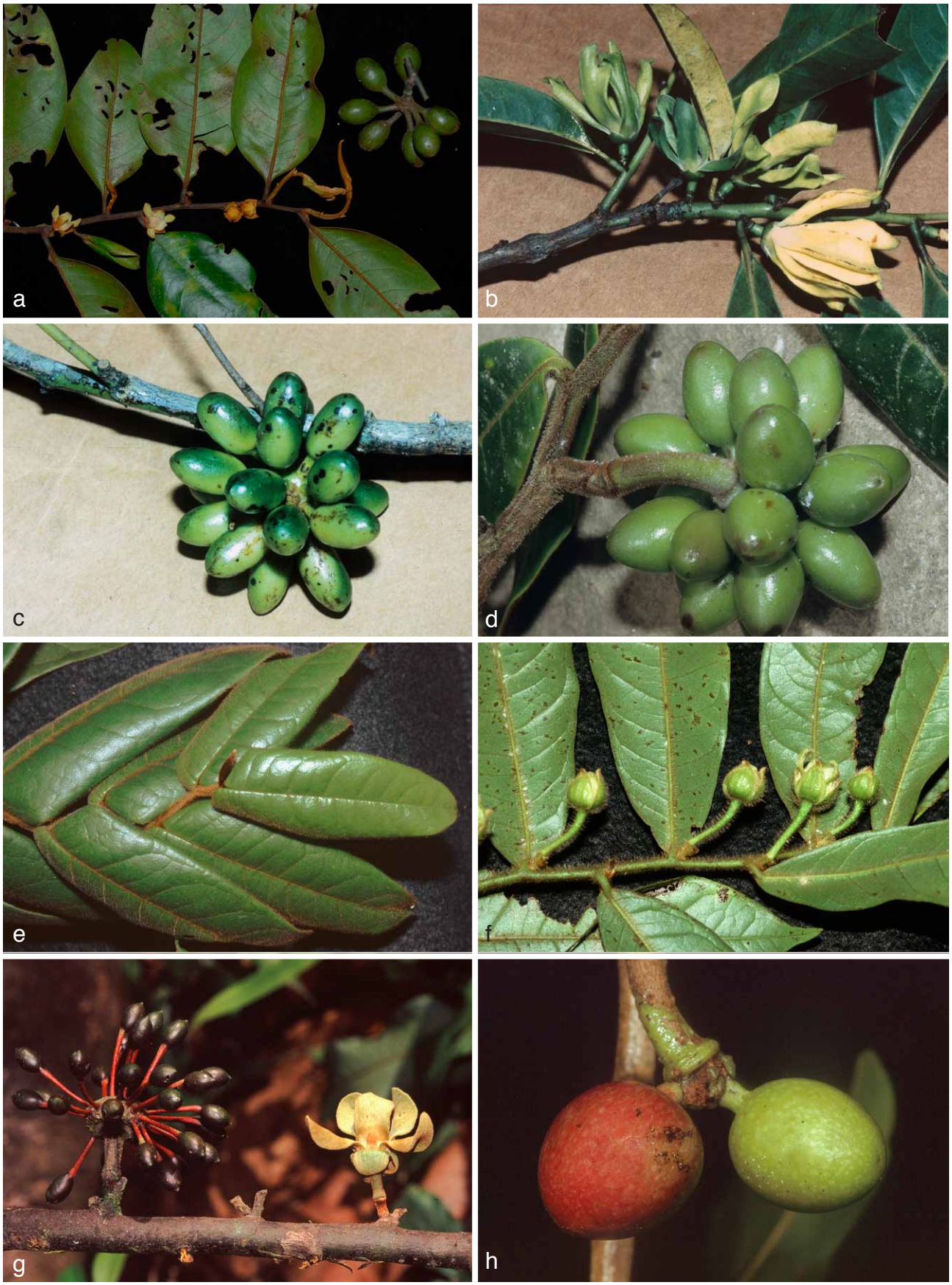


Plate 8 a. *Guatteria stipitata* R.E.Fr. Flowering branch and separate fruit. – b, c. *Guatteria subsessilis* Mart. b. Flowering branch; c. fruit. – d. *Guatteria talamancana* N.Zamora & Maas. Fruit. – e, f. *Guatteria tomentosa* Rusby. e. Vegetative branch; f. branch with flower buds. – g. *Guatteria ucayalina* Huber. Part of branchlet with flower and fruit. – h. *Guatteria verrucosa* R.E.Fr. Fruit (a: Ecuador, data lost; b, c: *Maas et al. 8684*; d: *Maas et al. 9476*; e: *Maas et al. 9521*; f: *Maas et al. 9555*; g: *Maas et al. 7817*; h: *Chatrou et al. 80*). — Photos: a: Unknown; b–g: P.J.M. Maas; h: L.W. Chatrou.

157. *Guatteria subsessilis* Mart. — Plate 8b, c; Map 35

Guatteria subsessilis Mart. (1841) 29, t. 9, f. I; R.E.Fr. (1939) 481, f. 25d, e; Steyerm. et al. (1995) 447. — Type: *Martius s.n.* (holo M), Brazil, Amazonas, Manaus ('Barra do Rio Negro'), Oct. 1819.

Tree or shrub 2–22 m tall, 5–30 cm diam; young twigs sparsely covered with appressed hairs, soon glabrous, black. *Leaves*: petiole 5–10 mm long, 1–3 mm diam; lamina narrowly elliptic, 10–25 by 3–9 cm (leaf index 2.6–5), chartaceous, not verruculose, shiny or dull, greyish, greyish green to brown above, brown to greyish green below, glabrous above, sparsely covered with appressed hairs mostly on primary vein to glabrous below, base acute to slightly attenuate, apex acute to acuminate (acumen 5–10 mm long), primary vein slightly raised to flat above, secondary veins distinct, 10–17 on either side of primary vein, slightly raised to flat above, smallest distance between loops and margin 1–6 mm, tertiary veins inconspicuous, slightly raised to flat above, reticulate. *Flowers* in 1–2(–3)-flowered inflorescences in axils of leaves or less often on leafless branchlets; pedicels 2–10 mm long, 1–1.5 mm diam, fruiting pedicels, 1–3 mm diam, glabrous, but part below articulation sparsely covered with appressed hairs, articulated at 0.3–0.6 from the base, bracts 5–6, soon falling, broadly ovate and c. 1 mm long at the base to transversely broadly ovate and c. 3 mm long at the top; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 2–5 by 2–6 mm, appressed, outer side sparsely covered with appressed hairs to glabrous; petals green, maturing cream or bright yellow in vivo, narrowly elliptic to narrowly ovate, 13–20{–40} by 2–9{–15} mm, outer side rather densely to sparsely covered with appressed to erect hairs; stamens 1–2 mm long, connective shield papillate. *Monocarps* 5–25, green, maturing dark maroon to purplish red in vivo, black in sicco, ellipsoid, 10–15 by 5–7 mm, glabrous, rarely sparsely covered with appressed hairs, apex rounded to apiculate (apiculum < 0.5 mm long), wall 0.1–0.5 mm thick, stipes 2–8 by 1 mm. *Seed* ellipsoid, 8–15 by 4–6 mm, pale brown, longitudinally and transversely grooved to rugose, raphe not distinct from rest of seed.

Distribution — Colombia (Antioquia), Venezuela (Amazonas, Apure, Bolívar), Guyana, Amazonian Brazil (Amazonas, Pará), Bolivia (Beni).

Habitat & Ecology — In periodically inundated (igapó or várzea) forest, on clayey or sandy soil, or (in Colombia) in premontane forest with *Quercus* as dominant tree. At elevations of 0–1650 m. Flowering: February to September; fruiting: January to April, October.

Vernacular names — Venezuela: Majagua, Majagua negra.

Notes — *Guatteria subsessilis* is one of the few species often occurring in periodically flooded igapó and várzea forests along rivers at low elevations, and less often on dry ground. It is well marked by coriaceous leaves in which the primary vein is often slightly raised on the upper side, very narrow petals, and by relatively short pedicels and stipes.

The Colombian material from Antioquia, however, occurs in premontane forest instead, but matches *G. subsessilis* in all morphological features.

158. *Guatteria synsepala* Maas & Westra, *sp. nov.* — Fig. 70c, 79; Map 34

Sepalis longe connatis foliis parvis, monocarpiis breviter stipitatis, seminibus fere laevibus bene distincta. — Typus: *Betancur et al. 811* (holo HUA 2 sheets; iso COL, F, MO, NY, U 2 sheets), Colombia, Antioquia, Mun. Amalfí, Cordillera Central, 8–15 km from Amalfí to Rumazón, sitios 'Salazar' and 'La Playa', 1550 m, 28 Sept. 1988.

Shrub, liana, or small tree of up to 8 m tall, c. 3 cm diam; young twigs rather densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 3–6 mm long, c. 1 mm diam; lamina narrowly elliptic, 6–13(–17) by 2–4(–7) cm (leaf index 2.5–3.6), chartaceous, not verruculose, dull, greyish brown to dark brown above, brown below, sparsely covered with appressed hairs, soon completely glabrous above, sparsely covered with appressed hairs below, base acute to attenuate, apex acute to acuminate (acumen c. 5 mm long), primary vein impressed above, secondary veins distinct, 8–10 on either side of primary vein, flat above, smallest distance between loops and margin 1–2 mm, tertiary veins slightly raised to flat above, reticulate to slightly percurrent. *Flowers* solitary in axils of leaves or less often on leafless branchlets; pedicels 5–10 mm long, 1–1.5 mm diam, fruiting pedicels 15–20 mm long, 1.5–2 mm diam, sparsely covered with appressed hairs, articulated at 0.2–0.4 from the base, bracts 4–6, soon falling, not seen; flower buds broadly ovoid; sepals connate, finally broadly ovate-triangular, c. 6 by 6 mm, appressed, outer side densely covered with appressed hairs; petals green, brown to black in vivo, ovate, 10–12 by 7–8 mm, outer side densely covered with appressed hairs; stamens c.1.5 mm long, connective shield papillate. *Monocarps* 10–30, maturing green, orange-green ('verde granate') to black in vivo, brown in sicco, ellipsoid, 8–15 by 6–10 mm, glabrous, apex apiculate (apiculum < 1 mm long), wall c. 0.5 mm thick, stipes 4–10 by 1–2 mm. *Seed* ellipsoid, 7–10 by 5–7 mm, brown, smooth to weakly pitted, raphe raised.

Distribution — Colombia (Antioquia).

Habitat & Ecology — No mention of vegetation type on the labels, but probably occurring in forests. At elevations of 1150–2030 m. Flowering: July, September, October; fruiting: September, December.

Vernacular names — Not recorded.

Other specimens examined. Colombia, **Antioquia**, Mun. Amalfí, Cordillera Central, 8–15 km from Amalfí to Rumazón, sitios 'Salazar' and 'La Playa', 1550 m, 28 Sept. 1988, *Betancur et al. 817* (F, MO 2 sheets, U 2 sheets); Mun. Amalfí, 8–27 km NE of Amalfí, along the road from Vetilla to Fraguas, sitios 'Salazar' and 'Marenga', 1150–1450 m, 7 Dec. 1989, *Callejas et al. 9109* (NY); Mun. Concepción, Vereda Pelaez-San Bartolome, Finca El Cardal, 2030 m, 22 July 1997, *F.A. Cardona et al. 252* (F, MO); Mun. Amalfí, Vereda Las Animas, 1500–1600 m, *Tuberquia et al. 837* (JAUM), *Tuberquia & Zapata 1021* (COL, JAUM), *Tuberquia & Carvajal 1065* (JAUM), *1243* (COL).

Note — *Guatteria synsepala* is a species restricted to the Cordillera Central in the Colombia Department of Antioquia, where it occurs at elevations between 1150 and 2030 m. It is a shrub, liana, or small tree characterized by connate sepals., leaves with relatively few secondary veins (8–10), and shortly stipitate monocarps with almost smooth seeds.

159. *Guatteria tacarcunae* Erkens & Maas, *sp. nov*. — Fig. 70d, 80; Map 35

Guatteriae darienensis affinis sed pedicellis et stipitibus minoribus ramulisque pilis adpressis nec erectis obtectis differt. — Typus: *Gentry & Mori 13678* (holo MO), Panama, Darién, top of Cerro Mali, 1400 m, 17 Jan. 1975.

Tree 5–20 m tall, diam not recorded; young twigs densely covered with erect hairs to c. 2 mm long, soon glabrous. *Leaves*: petiole 5–10 mm long, 1–3 mm diam; lamina elliptic to narrowly elliptic, 8–20 by 4–7 cm (leaf index 2–3.2), chartaceous, not verruculose, shiny, greyish brown to brown above, brown below, rather densely covered with appressed hairs above, soon completely glabrous, sparsely to rather densely covered with appressed hairs to c. 2 mm long below, base acute to obtuse, apex acute to acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 7–12 on either side of primary vein, slightly impressed above, smallest distance between loops and margin 1–2 mm, tertiary veins slightly raised to flat above, percurrent. *Flowers* in 1-flowered inflorescences in axils of leaves; pedicels 15–30 mm long, 1–1.5 mm diam, fruit-

Fig. 79 *Guatteria synsepala* Maas & Westra. Flowering branch (*Betancur et al. 811*, isotype F).

Fig. 80 *Guatteria tacarcunae* Maas & Erkens. Flowering branch (*Gentry & Mori 13678*, holotype MO).

ing pedicels 1.5–2 mm diam, densely covered with erect hairs, articulated at 0.2–0.3 from the base, bracts 5–6, soon falling, not seen; flower buds depressed ovoid; sepals basally free, broadly to shallowly ovate-triangular, 4–6 by 4–7 mm, finally reflexed, outer side densely covered with appressed hairs; petals green in vivo, elliptic-oblong, 10–20 by 5–7 mm, outer side densely covered with appressed hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* (only young ones seen) 25–50, greenish white with red stripes to green in vivo, brown in sicco, ellipsoid, 5–7 by 3–5 mm, sparsely covered with appressed hairs, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 3–10 by 1 mm. *Seed* not seen.

Distribution — Panama (Darién).

Habitat & Ecology — In lower montane forest or tropical wet forest. At elevations of 1400–1600 m. Flowering: January, February; fruiting: January, February, July.

Vernacular names — Not recorded.

Other specimens examined. Panama, **Darién**, Cerro Mali, 10 year old second growth on site of Old Helipad, 17 Jan. 1975, *Gentry & Mori 13660* (MO); vicinity Cerro Tacarcuna, summit camp, along stream N of camp, 1550–1600 m, 1 Feb. 1975, *Gentry & Mori 14052* (MO); Cerro Tacarcuna W ridge, trail toward Río Pucura, just below summit camp, 1500–1600 m, 2 Feb. 1975, *Gentry & Mori 14123* (MO); idem, 5 Feb. 1975, *Gentry & Mori 14149* (MO); S slope of westernmost peak of Cerro Tacarcuna massif, 1500–1600 m, 22 July 1976, *Gentry et al. 16953* (MO).

Note — *Guatteria tacarcunae* looks quite similar to *G. darienensis*, differing only in shorter pedicels (15–30 vs 30–60 mm) and shorter stipes (3–10 vs 7–15 mm) and having its young twigs covered with erect instead of appressed hairs. *Guatteria tacarcunae* is, moreover, found at higher elevations (1400–1600 vs 20–800 m).

160. *Guatteria talamancana* N.Zamora & Maas — Plate 3g, h, 8d; Map 33

Guatteria talamancana N.Zamora & Maas (2000) 241, f. 1, 2. — Type: *Aguilar & Morales 4453* (holo INB; iso K, MO, U), Costa Rica, San José, Cantón de Pérez Zeledón, Parque Nacional Chirripó, Cordillera de Talamanca, Finca Los Romeros, main trail, 'Fila cementerio de la maquina', 1700 m, 22 Jan. 1996.

Tree 2.5–20 m tall, 15–30 cm diam; young twigs very densely covered with long-persisting, erect, brown hairs to c. 2 mm long. *Leaves*: petiole 2–5 mm long, 3–4 mm diam; lamina narrowly oblong-elliptic, sometimes narrowly obovate, 13–23 by 3.5–8 cm (leaf index 2.8–3), coriaceous, densely verruculose, dull, greyish to greyish brown above, brown below, glabrous above, but primary vein densely covered with erect, brown hairs, densely covered with erect, brown hairs below, base obtuse, basal margins often revolute, apex acuminate (acumen 5–15 mm long), primary vein flat to slightly raised above, secondary veins distinct, 7–17 on either side of primary vein, flat to slightly raised above, smallest distance between loops and margin 2–3 mm, tertiary veins inconspicuous, flat above, reticulate. *Flowers* solitary in axils of leaves; pedicels 15–30 mm long, c. 3 mm diam, fruiting pedicels 30–55 mm long, 5–6 mm diam, densely covered with erect, brown hairs, articulated at 0.2–0.3 from the base, bracts 1–2, foliaceous, 25–30 mm long, outer side densely covered with erect, brown hairs; flower buds conical, sepals basally connate, ovate-triangular to broadly ovate-triangular, 15–20 by 10–15 mm, appressed, outer and inner side densely covered with erect, brown hairs; petals yellow or cream in vivo, ovate-oblong, 15–25 by 10–12 mm, outer side densely covered with appressed, brown hairs; stamens c. 1.5 mm long, connective shield hairy. *Monocarps* 10–15, black in vivo, black in sicco, ellipsoid to ovoid, 20–30 by 18–20 mm, glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 2–3 by 2–3 mm. *Seed* ellipsoid, 8–11 by 5–6 mm, dark brown, pitted to rugulose, raphe not distinct from rest of seed.

Distribution — Costa Rica, Panama.

Habitat & Ecology — In forest. At elevations of 1000–2000 m. Flowering: August, September, December; fruiting: March, April, December.

Vernacular names — Not recorded.

Note — *Guatteria talamancana*, a species occurring at high elevations up to 2000 m, can be recognized by its indument of long-persisting, very long, erect, brown hairs on most of its parts and by long sepals (15–20 mm long). It has been confused with *G. elegantissima*, from which it differs by its much larger sepals (15–20 vs 5–7 mm) and monocarps (20–30 vs 5–8 mm), different leaf shape and size, and its occurrence at higher elevations (1000–2000 m vs 0–350 m).

161. *Guatteria tenera* R.E.Fr. — Map 35

Guatteria tenera R.E.Fr. (1939) 359, f. 8c, d. — Type: *Stork 2598* (holo F; iso S fragment), Costa Rica, San José, Santa Clara Hills, 1500 m, 16 June 1928.

Tree 3–8 m tall, diam not recorded; young twigs rather densely to sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2–5 mm long, 0.5–1 mm diam; lamina narrowly elliptic, 7–12 by 2–3 cm (leaf index 3.5–4), chartaceous, sparsely verruculose or not on both sides, shiny or dull, brownish grey above, brown below, glabrous above, sparsely covered with appressed hairs below, base acute, apex acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 11–15 on either side of primary vein, impressed to slightly raised above, smallest distance between loops and margin c. 1 mm, tertiary veins flat or slightly raised above, reticulate to percurrent. *Flowers* solitary in axils of leaves; pedicels 10–20 mm long, rather densely to sparsely covered with appressed to less often erect hairs, articulated at 0.1–0.3 from the base, bracts 4–6, soon falling, not seen; flower buds broadly ovoid, shortly pointed, sepals broadly ovate-triangular, 3–4 by 3–4 mm, reflexed, outer side densely covered with appressed hairs; petals greenish yellow in vivo, ovate, 7–12 by 3–5 mm, outer side densely covered with appressed hairs; stamens 1–1.5 mm long, connective shield papillate. *Monocarps* and *seed* unknown.

Distribution — Costa Rica.

Habitat & Ecology — In non-inundated forest. At elevations of 1500–1600 m. Flowering: April, June, July; fruiting: unknown.

Vernacular names — Not recorded.

Note — *Guatteria tenera* has only been collected twice so far. It is characterized by very narrow leaves with the veins impressed on the upper side. It possibly represents a narrow-leaved form of *G. amplifolia*.

162. *Guatteria terminalis* R.E.Fr. — Map 34

Guatteria terminalis R.E.Fr. (1938) 709; (1939) 303, f. 2a, b; Maas & Westra (2010) 272, pl. 2. — Type: *Lechler 2648* (holo UPS; iso B, G 2 sheets, K, LE, P), Peru, Puno, Tatanera ('Tatanara'), Aug. 1854.

Tree or shrub 1–12 m tall, 15–25 cm diam; young twigs rather densely to sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2–8 mm long, 0.5–1 mm diam; lamina narrowly elliptic, 3.5–9 by 1.5–3.5 cm (leaf index 2.2–2.7), coriaceous, not verruculose, shiny, dark blackish brown above, dark brown below, glabrous above, sparsely covered with appressed, white hairs below, base long-attenuate, apex obtuse, acute, or shortly acuminate (acumen 3–7 mm long), primary vein flat to impressed above, secondary veins distinct, 7–12 on either side of primary vein, strongly raised above, smallest distance between loops and margin 1–2 mm, tertiary venation strongly raised above, reticulate. *Flowers* solitary, terminal

on leafy branchlets or most often terminal on leafy axillary branchlets; pedicels 10–20 mm long, c. 1 mm diam, fruiting pedicels to c. 2 mm diam, rather densely to sparsely covered with appressed, white hairs, articulated at or somewhat above the base, bracts not present or not detectable, the leaves close to the flower generally smaller than leaves on vegetative branchlets at most, but of comparable shape; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–5 by 3–5 mm, reflexed, outer side rather densely or densely covered with appressed hairs; petals lead-coloured, greenish yellow or yellow in vivo, narrowly elliptic to narrowly obovate, 10–20 by 4–8 mm, outer side densely covered with appressed hairs; stamens 1–2 mm long, connective shield papillate. *Monocarps* 20–25, green, maturing purple-red ('morado') in vivo, black in sicco, ellipsoid, 12–17 by 6–7 mm, sparsely covered with appressed hairs, apex apiculate (apiculum slightly pointed and to c. 1 mm long), wall c. 0.2 mm thick, stipes 1–4 by 2–3 mm. *Seed* ellipsoid, brown, 10–11 by 4–5 mm, smooth to pitted, raphe not distinct from rest of seed.

Distribution — Peru (Cusco, Huánuco, Pasco, Puno, Ucayali).

Habitat & Ecology — In cloud forest, dominated by *Cyatheaceae*, *Alzateaceae*, *Cunoniaceae* and *Myrtaceae*, or low elfin forest with many epiphytic lichens, mosses, and ground covered by a thick layer of roots, rotten leaves and mosses. At elevations of 1795–2300 m. Flowering: February, June, August to November; fruiting: February, August to October.

Vernacular names — Not recorded.

Notes — *Guatteria terminalis* is the only South American species with terminal flowers. Terminal flowers in *Guatteria* otherwise are only known in *G. acrantha* and *G. grandiflora*, from Central America and from Mexico and Central America, respectively.

The lead-coloured flowers reported by Farfán are a curious feature of this species, but more observations on this aspect are desirable.

No proper bracts could be found below the flowers. The articulation of the pedicels is usually seen a little above the uppermost leaf. As compared to the bulk of *Guatteria* species, one might expect two (small) bracts together with the articulation, one on either side. Being unable to find such bracts or even traces of them in the material we studied, we feel we cannot confirm either their presence or absence.

163. *Guatteria tomentosa* Rusby — Plate 8e, f; Map 36

Guatteria tomentosa Rusby (1910) 504; R.E.Fr. (1939) 348, t. 18. — Type: *R.S. Williams 753* (holo NY), Bolivia, La Paz, Tumupasa, 500–600 m, 11 Dec. 1901.

Guatteria trichoclonia Diels (1931) 77; R.E.Fr. (1939) 347, t. 17. — Type: *Buchtien 698* (holo B; iso F, S, US), Bolivia, La Paz, Mapiri, San Carlos, 24 Nov. 1926.

Guatteria setosa Rusby (1934) 55. — Type: *Tate 1138* (holo NY; iso NY), Bolivia, La Paz, Chuquini, 1000 m ('3000 ft'), 17–19 April 1926.

Guatteria sp. 14 Chatrou et al. (1997) 111.

Tree or sometimes a shrub 2–20(–25) m tall, to c. 30 cm diam; young twigs densely covered with long-persisting erect, brown, stiff hairs ('hirsute') to c. 3 mm long. *Leaves*: petiole 2–5 mm long, 1–3 mm diam; lamina narrowly ovate to narrowly obovate, sometimes elliptic, 7–23 by 2–6 cm (leaf index 1.9–5.5), chartaceous, not verruculose, dull, brown, greyish green or black above, brown or greenish below, sparsely to densely covered with erect, brown, stiff hairs ('hirsute') to c. 3 mm long to glabrous above, but primary vein mostly permanently hairy, densely covered with erect, brown, stiff hairs ('hirsute') to c. 3 mm long below, base sometimes oblique, obtuse to cordate, sometimes acute or even stem-clasping, basal margins often revolute, apex acuminate (acumen 5–35 mm long), rarely acute, obtuse, or even emarginate, primary vein impressed to flat above, secondary veins distinct, 6–15 on either side of primary vein, flat to raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves or sometimes on leafless branchlets; flowering and fruiting pedicels 10–50(–70) mm long, 1–3 mm diam, densely covered with long-persisting erect, brown, stiff hairs ('hirsute') to c. 3 mm long, articulated at 0.1–0.4 from the base, bracts 5–6, soon fallling or sometimes persisting, the uppermost bracts sometimes foliaceous, narrowly elliptic, 6–20 mm long, the basal ones rarely more or less foliaceous, very broadly ovate, 4–5 mm long; flower buds depressed ovoid, slightly pointed; sepals free, broadly ovate-triangular, 5–13 by 5–10 mm, appressed, but finally reflexed, outer side densely covered with long-persisting erect, brown, stiff hairs ('hirsute') to c. 3 mm long; petals green, maturing yellow or cream in vivo, ovate-triangular to obovate or narrowly so, 15–30 by 6–15 mm, outer side densely covered with appressed and erect, greyish to brown hairs; stamens 1–2 mm long, connective shield glabrous. *Monocarps* 10–75, green, maturing purple-black to black in vivo, black or brown in sicco, ellipsoid, 6–10 by 3–7 mm, sparsely covered with erect to appressed hairs to glabrous, apex apiculate (apiculum 0.5–1 mm long), wall 0.1–0.2 mm thick, stipes 4–20 by 0.5–1 mm. *Seed* ellipsoid, 6–10 by 3–5 mm, dark brown, pitted, raphe raised.

Distribution — Honduras, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Boyaca, Chocó, Cundinamarca), Ecuador (Morona-Santiago, Napo, Sucumbios), Peru (Amazonas, Cusco, Huánuco, Junín, Madre de Dios, Pasco, San Martín, Ucayali), Brazil (Acre, Amazonas, Bahia, Espírito Santo, Minas Gerais), Bolivia (Cochabamba, La Paz, Pando).

Habitat & Ecology — In primary or secondary, non-inundated forest or periodically inundated forest, rarely in low cloud forest, on clayey to sandy soil. At elevations of 0–1700 m. Flowering: throughout the year; fruiting: mainly from July to December.

Vernacular names — Bolivia: Piraquina (*Killeen 4450*), Piraquina de barbecho (*Meneces 607*), Piraquina peluda de barbecho (*Hartshorn & Meneces 2332*). Brazil: Envira-da-folha-peluda (*Waltier et al. 11*). Peru: Gana vara (*Schunke V. 10026*), Millua hicoja (*Schunke V. 7427*).

Notes — *Guatteria tomentosa* is very well recognizable by the long-persistent indument of erect, stiff hairs, pointed flower buds and long sepals of 5–13 mm long. The leaf base of this species is extremely variable. It goes from obtuse, cordate to even stem-clasping, and is often oblique. It could be confused with *G. hirsuta*, but from that species it differs by its erect instead of erect and appressed indument on most parts of the plant, and by often revolute basal leaf margins.

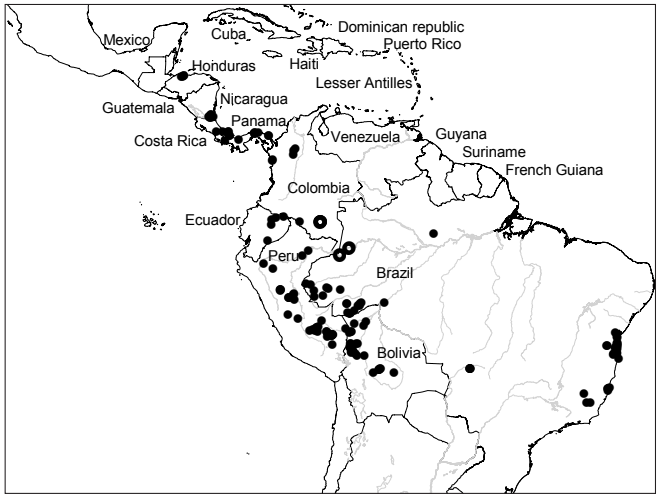
Three collections from Chocó, Colombia (*Espina Z. et al. 2975* (MO, U), *García C. & Agualimpia 376* (MO, U) and *Ramirez & Evans 3993* (JAUM) are aberrant in having much larger leaves (18–20 by 7 cm) and by having densely hirsute and strongly pointed monocarps. They possibly represent an undescribed species.

164. *Guatteria trichocarpa* Erkens & Maas — Map 36

Guatteria trichocarpa Erkens & Maas (2008) 404; Maas & Westra (2011) 139, f. 21, 22. — *Guatteriella tomentosa* R.E.Fr. (1939) 541, f. 39; Murillo A. & Restrepo (2000) 124, f. 38. — Type: *Ducke RB 23916* (holo S; iso RB, SPF), Brazil, Amazonas, São Paulo de Olivença, Rio Solimões, 25 Feb. 1932; not *Guatteria tomentosa* Rusby (1910).

Tree or shrub 3–20 m tall, 11–80 cm diam; young twigs densely covered with a velutinous indument of erect and appressed, long-persistent hairs. *Leaves*: petiole 5–10 mm long, 1–4 mm diam; lamina narrowly oblong-ovate, 18–30 by 4–8 cm (leaf

Fig. 81 *Guatteria trichostemon* R.E.Fr. Flowering branch (*Krukoff 8862*, isotype U).



Map 36 Distribution of *Guatteria tomentosa* (●) and *G. trichocarpa* (⊙).

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, tertiary veins raised above, percurrent to reticulate. *Flowers* solitary in axils of leaves; pedicels 5–12 mm long, c. 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 or 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 hairy. *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 grooved, raphe not distinct from rest of seed.

Distribution — Amazonian Colombia (Amazonas), Brazil (Amapá, 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: January, December; fruiting: November.

Vernacular names — Colombia: Buruchicú (Muinane name) (*Londoño et al. 1444*), Butruchicu (Muinane name) (*Murillo A. & Rodríguez A. 538*), Kïyïmeko (Miraña name), Palo de buho (*Londoño et al. 1444*).

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 other species of *Guatteria*.

165. *Guatteria trichostemon* R.E.Fr. — Fig. 81; Map 37

Guatteria trichostemon R.E.Fr. (1939) 474, f. 24e. — Type: *Krukoff 8862* (holo S; iso BM, F, G, K, LE, MO, NY, P, U, US), Brazil, Amazonas, Basin of Rio Solimões, Mun. São Paulo de Olivença, Basin of Creek Belém, 26 Oct.–11 Dec. 1936.

Tree c. 20 m tall, c. 7.5 cm diam; young twigs rather densely covered with curly, erect and appressed, brown hairs, soon glabrous. *Leaves*: petiole 5–7 mm long, c. 1 mm diam; lamina narrowly elliptic, 6–10 by 2–3 cm (leaf index 2.6–3), chartaceous, not verruculose, shiny, dark blackish brown above, dark brown below, glabrous, but primary vein densely covered with erect, brown hairs above, sparsely to rather densely covered with curly, erect and appressed, brown hairs below, base attenuate, apex acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 10–12 on either side of primary vein, raised above, smallest distance between loops and margin 2–4 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 25–30 mm long, c. 0.5 mm diam, rather densely covered with curly, erect and appressed, brown hairs, articulated at 0.3–0.5 from the base, bracts c. 5, soon falling, not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–5 by 3–5 mm, apical part reflexed, outer side rather densely covered with appressed hairs; petals colour not recorded, oblong-elliptic, 7–10 by 4–5 mm, outer side densely covered with curly, erect and appressed, brown hairs; stamens c. 1 mm long, connective shield hairy. *Monocarps* and *seed* not seen.

Distribution — Amazonian Brazil (Amazonas).

Habitat & Ecology — In non-inundated forest. At an elevation of c. 100 m. Flowering: October to December; fruiting: unknown.

Vernacular names — None.

Note — *Guatteria trichostemon*, only known from the type collection, is well recognizable by its attenuate leaf base, long and slender pedicels, and a hairy connective shield. Fries placed this species in the small sect. *Trichostemon* (together with *G. foliosa*, *G. maypurensis* and *G. polyantha*), which had as its main features a hairy connective shield, small leaves and long-stipitate monocarps. He compared *G. trichostemon* with *G. stenopetala*, but from that species it clearly differs by thinner and distinctly attenuate leaves.

166. *Guatteria ucayalina* Huber — Fig. 70e; Plate 8g; Map 37

Guatteria ucayalina Huber (1906) 560; R.E.Fr. (1938) 717; (1939) 448, f. 20a. — Type: *J. Huber 1431* (holo MG; iso F, P), Peru, Ucayali, Quebrada Grande del Cerro de Canchahuaya, 12 Nov. 1898.

Guatteria boliviana H.J.P.Winkl. (1909) 242; R.E.Fr. (1939) 400, syn. nov. — Type: *Buchtien 52* (holo B; iso E, F, G, GH, L, NY), Bolivia, La Paz, San Carlos de Mapiri, 750 m, Sept. 1907.

Guatteria speciosa R.E.Fr. (1939) 401, syn. nov. — Type: *Ducke RB 29049* (holo S; iso K, MO, NY, RB 2 sheets), Brazil, Amazonas, Rio Negro, near mouth of Rio Curicuriari, 16 Nov. 1936.

Guatteria lawrancei R.E.Fr. (1939) 401, syn. nov. — Type: *Lawrance 215* (holo S; iso A, BM, F, G, K, MO, NY, US 2 sheets), Colombia, Boyacá, Mt Chapon, NW of Bogotá, '3400 ft', 14 June 1932.

Guatteria recurvisepala R.E.Fr. (1939) 447, f. 19e; Murillo A. & Restrepo (2000) 110, f. 32, syn. nov. — Type: *Skutch 4234* (holo S; iso K 2 sheets, MO 2 sheets, NY, S, US), Costa Rica, San José, vicinity of El General, 670 m, Feb. 1939.

Guatteria longepetiolata R.E.Fr. (1948b) 6, syn. nov. — Type: *Cuatrecasas 9185* (holo US; iso COAH, COL 2 sheets, F, S fragment), Colombia, Caquetá, Cordillera Oriental, Sucre, Quebrada de La Calaña, 1000–1100 m, 6 Apr. 1940.

Guatteria macropetala R.E.Fr. (1948b) 7, syn. nov. — Type: *Cuatrecasas 8883* (holo US; iso COAH, COL, F), Colombia, Caquetá, Florencia, Buenavista, 450 m, 30 Mar. 1940.

Guatteria cardoniana R.E.Fr. (1948b) 9, syn. nov. — Type: *Cardona 1196* (holo US), Venezuela, Bolívar, source of Río Caroní, near mouth of Río Tirika ('Orillas del Caroní, cerca de la boca Tirika'), 350 m, May 1945.

Guatteria schunkevigoi D.R.Simpson (1975) 307, syn. nov. — Type: *Schunke V. 3551* (holo F; iso COL, F, G, MO, NY, S, US), Peru, San Martín, Prov. Mariscal Caceres, Distr. Campanilla, road to Las Achiras, SW of Caserío Sión, 23 Oct. 1969.

Guatteria sp. 9 Chatrou et al. (1997) 111.

Tree or rarely a shrub 2–35 m tall, to c. 80 cm diam; young twigs densely covered with long-persisting, erect, brown hairs,

finally becoming glabrous. *Leaves*: petiole 5–15 mm long, 2–5 mm diam; lamina narrowly elliptic to narrowly ovate, rarely narrowly obovate, or ovate to elliptic, 10–36 by 4–17 cm (leaf index 2–4.2), coriaceous to chartaceous, not verruculose, dull, greyish to greyish black above, brownish below, primary vein densely to sparsely covered with erect, brown hairs to glabrous above, further sparsely hairy to glabrous, densely to rather densely, rarely sparsely covered with erect or rarely appressed, brown hairs below, base obtuse to acute, apex acuminate (acumen 5–30 mm long) to acute, primary vein impressed to flat above, secondary veins distinct, 11–22 on either side of primary vein, impressed to slightly raised above, smallest distance between loops and margin 1–5 mm, tertiary veins flat to slightly raised above, percurrent to less often reticulate. *Flowers* in 1–3(–7)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–45 mm long, 1–2 mm diam, fruiting pedicels to c. 3 mm diam, densely covered with erect, brown hairs, articulated at 0.2–0.4 from the base, bracts 5–7, soon falling, elliptic to broadly elliptic, basal bracts c. 2 mm long, upper ones to c. 9 mm long; flower buds depressed ovoid, sometimes slightly pointed; sepals free, broadly ovate-triangular, 4–11 by 4–11 mm, soon strongly reflexed, outer side densely covered with erect to sometimes appressed, brown hairs; petals green, maturing yellow in vivo, ovate to obovate, or narrowly so, 20–45 by 7–25 mm, outer side densely covered with appressed and erect, brown hairs; stamens 1.5–2 mm long, connective shield papillate, sometimes slightly umbonate. *Monocarps* 40–75, green, maturing purple-black to black in vivo, black in sicco, ellipsoid, 7–12{–15} by 5–8 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum 0.1–0.5 mm long), wall 0.1–0.3 mm thick, stipes 8–50 by 0.5–1 mm. *Seed* ellipsoid, 6–12 by 4–7 mm, pale to dark brown, smooth to pitted, raphe flat.

Distribution — Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Bolívar, Caquetá, Chocó, Guainía, Huila, Meta, Norte de Santander, Vaupés),Venezuela (Amazonas, Apure, Barinas, Bolívar, Carabobo, Merida, Táchira, Zulia), Guyana, Suriname, Ecuador (Morona-Santiago, Napo, Pastaza, Sucumbios, Zamora-Chinchipe), Peru (Amazonas, Cusco, Huánuco, Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), Brazil (Acre, Amazonas, Rondônia), Bolivia (Cochabamba, La Paz, Pando).

Habitat & Ecology — In non-inundated forest, sometimes in edges of savannas or lajas (Venezuela), on clayey to sandy soil. At elevations of 100–1800 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Bolivia: Chojñamora (*Buchtien 52*), Piraquina negra (*Hartshorn & Meneces 2067*, *Meneces 2067*, *D.N. Smith et al. 13699*). Brazil: Envira-fofa-da-folha-grande (*Daly et al. 9710*), Envireira (*Daly et al. 6762*). Colombia: Garrapato (*Cogollo et al. 4302*, *Fonnegra et al. 3062*, *3130*, *López A. 877*), Pá-ma (Kabuyarí name) (*Schultes & Cabrera R. 15373*). Costa Rica: Mahagua (*Hartshorn 1799*). Ecuador: Gañitahue (Huaorani name) (*M. Aulestia & Gonti 2009*), Goi tahuemo (Huaorani name) (*M. Aulestia et al. 1774*), Oñitahue (Huaorani name) (*M. Aulestia 3062*), Oñitahuemo (Huaorani name) (*M. Aulestia & Quihuiamo 3176*). Peru: Caruhuasca (*Kröll & Tello 870*, *Tello 1687*), Caruhuasca blanca (*Tello 1801*), Caruhuasca (*Melo 10*), Hicoja negra (*Schunke V. 3551*, *5455*), Quiyamas (*D.N. Smith 5193*), Wampu yais (Shuar name) (*Tunqui 184*), Wámpu yéis (Shuar name) (*Huashikat 714*, *1004*, *1628*), Yais (Shuar name) (*Kajekai 914*, *Vásquez et al. 24152*), Yumí yeis (Shuar name) (*Huashikat 249*). Venezuela: Anon (*Veillon 115*), Cabo de pala (*Bunting et al. 6753*, *6932*, *7513*, *8385*), Escobo (*Ara 28*), Karawri-yék (Arekuna name) (*F. Cardona 1196*), Majaguillo negro (*J.O. Ramirez & Paredes 75*), Tairu (Barí name) (*Lizarralde 229*), Verdecito (*Steyermark et al. 101312*).

Uses — Colombia: fruits used medicinally for cold. Alkaloid slightly positive (*Schultes et al. 24393*).

Notes — *Guatteria ucayalina* is well recognizable by a combination of a dense indument of brown, erect hairs on young twigs, lower side of leaves and pedicels, a mostly greyish upper leaf side, strongly recurved sepals, and long-stipitate monocarps. The leaf indument is variable from dense in most specimens to rather dense or sparse in mainly Venezuelan collections.

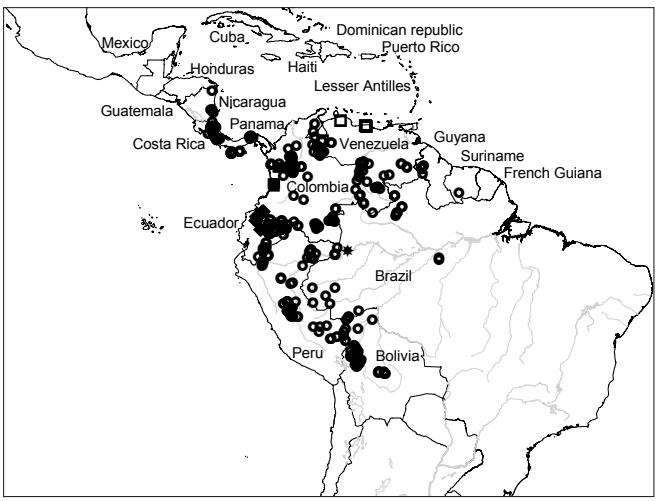
Guatteria ucayalina is widely distributed, ranging from Central America in the north (where it was previously known as *G. recurvisepala*) to Bolivia in the south, and Venezuela and Guyana in the east.

The only specimen from the Atlantic coast of Colombia (*Forero 9699* from Chocó) is aberrant by monocarps with an apiculum of c. 1 mm long, whereas it otherwise never exceeds 0.5 mm in this species.

167. *Guatteria vallensis* Maas & Westra, *sp. nov.* — Fig. 70f, 82, 83; Map 37

Foliis parvis angustis verruculosis petalisque angustis inaeqalis bene distincta. — Typus: *Monsalve B.685* (holo U; iso CUVC, JAUM, MO), Colombia, Valle del Cauca, Bajo Calima, Concesión Pulpapel/Buenaventura, 100 m, 20 Feb. 1985.

Tree 5–25 m tall, diam not recorded; young twigs rather densely covered with appressed to half-appressed hairs, soon glabrous. *Leaves*: petiole 3–7 mm long, c. 1 mm diam; lamina narrowly elliptic, 8–11 by 2–3 cm (leaf index 2.8–4), chartaceous, densely or rarely sparsely verruculose, dull, dark brown to brown above, brown to green below, glabrous above, sparsely covered with appressed hairs, mainly along primary vein, below, base acute to attenuate, apex acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 12–15 on either side of primary vein, slightly raised above, smallest distance between loops and margin 3–4 mm, tertiary veins slightly raised above, reticulate. *Flowers* solitary in axils of leaves or on leafless branchlets; flowering and fruiting pedicels 25–40 mm long, 1–1.5 mm diam, sparsely covered with appressed hairs, articulated at 0.1–0.2 from the base, bracts 5–6, soon falling, not seen; flower buds not seen; sepals free, broadly ovate-triangular, 3–4 by 3–4 mm, reflexed, outer side rather densely covered with appressed hairs; petals green, maturing yellow or cream in vivo, unequal, narrowly oblong-elliptic, 13–25 by 3–8 mm, the inner ones half as long as the outer ones (always?), outer side rather densely to sparsely covered with appressed



Map 37 Distribution of *Guatteria trichostemon* (✱), *G. ucayalina* (●), *G. vallensis* (■), *G. venezuelana* (□) and *G. venosa* (◆).

Fig. 82 *Guatteria vallensis* Maas & Westra. Fruiting branch (*Monsalve B.685*, isotype MO).

Fig. 83 *Guatteria vallensis* Maas & Westra. Flowering branch (old incomplete flower) (*Monsalve B.685*, holotype U).

hairs; stamens c. 1.5 mm long, connective shield papillate to glabrous. *Monocarps* 20–50, green in vivo, black in sicco, ellipsoid, 5–8 by 3–4 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.3 mm thick, stipes 5–15 by 0.5–1 mm. *Seed* ellipsoid, 5–8 by 3–4 mm, dark, shiny brown, pointed, pitted to rugulose, raphe not distinct from rest of seed.

Distribution — Western Colombia (Chocó, Valle del Cauca).

Habitat & Ecology — In non-inundated, pluvial, primary or secondary forest, on yellow to yellowish grey clay or loam. At elevations of 0–150 m. Flowering: January, February; fruiting: January, February, July, September, October.

Vernacular name — Colombia: Cargadero (*Faber-Langendoen & Rentería A. 1375*, *Gentry et al. 48341*, *Monsalve B.325*, *685*).

Other specimens examined. Colombia, **Chocó**, Quibdó-Guayabal road, 3–6 km N of Quibdó, 50 m, *Gentry & Rentería A. 24148* (MO, U); trail from Tutunendo-Quibdó road to Tubadó, c. 14 km NE of Quibdó, 90 m, *Gentry & Rentería A. 24474* (U); Mun. Quibdó, along road from Quibdó to Guayabal, *Espina Z. et al. 1494* (U). **Valle del Cauca**, Bajo Calima Concesión, c. 15 km NW of Buenaventura, 1 km past Luchin/Lijal intersection, on Luchin/Juanchaco area, 50 m, *Faber-Langendoen & Rentería A. 1001* (U); Bajo Calima Concesión, c. 20 km N of Buenaventura, 2 km past Pulpapel Station at km 13 of main road, 50 m, *Faber-Langendoen & Rentería A. 1375* (U); Bajo Calima Concesión, c. 25 km NW of Buenaventura, c. 9 km NW of San Isidro intersection on 'Canalete' near gate, 50 m, *Faber-Langendoen & Hurtado 1695* (U); Bajo Calima, road to Juanchaco Palmeras, 50 m, *Gentry et al. 48341* (CUVC, MO, U); Bajo Calima, Concesión Pulpapel/Buenaventura, 100 m, *Monsalve B.325* (MO, U).

Notes — *Guatteria vallensis* characteristically is a small and narrow-leaved species with unequal and very narrow petals. The leaves vary from densely to sparsely verruculose.

In *Monsalve B.685* (MO), the isotype collection, the petals are strongly unequal, the outer ones being twice as large as the inner ones (25 by 8 vs 11 by 4 mm).

We have not included the measurements of three sterile collections which are aberrant in having larger and relatively narrow leaves (13–16 by 2–4 cm) and a more attenuate leaf base.

168. *Guatteria venezuelana* R.E.Fr. — Fig. 70g, 84; Map 37

Guatteria venezuelana R.E.Fr. (1941) 110, f. 1e, f. — Type: *Delgado 180* (holo VEN; iso F 2 sheets, G, K, S 2 sheets, US), Venezuela, Distrito Federal, 'Bosques del Papelón', Avila, above Caracas, 7 June 1938.

Tree 5–15 m tall, 15–40 cm diam; young twigs densely covered with erect, mostly curly, brown hairs, mostly soon glabrous. *Leaves*: petiole 4–6 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly ovate, 5–11 by 2–4 cm (leaf index 2–3), coriaceous, not verruculose, shiny, greyish to greyish black above, pale brown below, glabrous above, but sparsely covered with erect, mostly curly, brown hairs when very young, sparsely covered with erect, mostly curly, brown hairs to glabrous below, base acute, distinctly attenuate, apex acuminate (acumen 5–15 mm long), primary vein flat to slightly raised above, secondary veins distinct, 8–10 on either side of primary vein, distinctly raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 15–30 mm long, c. 1 mm diam, fruiting pedicels to c. 2 mm diam, densely covered with erect, mostly curly, brown hairs, articulated at 0.2–0.4 from the base, bracts 5–7, soon falling, basal one c. 1 mm long, uppermost one to c. 2 mm long, probably much longer to judge by photograph; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–6 by 4–6 mm, reflexed, outer side densely covered with erect, mostly curly, brown hairs; petals green, inner side yellowish, base purplish red in vivo, elliptic to narrowly elliptic, 15–20 by 6–10 mm, outer side densely covered with erect, mostly curly, brown hairs; stamens c.1.5 mm long, connective shield papillate. *Monocarps* 30–50, green, maturing black in vivo, black in sicco, ellipsoid, 9–14 by 5–6 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.3–0.5 mm thick, stipes 0–5 by c. 1 mm. *Seed* ellipsoid, 9–11 by 4–6 mm, dark, shiny brown, rugulose, raphe not distinct from rest of seed.

Distribution — Northern Venezuela (Distrito Federal, Falcón, Mérida, Miranda, Sucre, Táchira).

Habitat & Ecology — In non-inundated, montane forest ('selva siempreverde'), one collection from 'pináculos calcáreos' (*Steyermark 99141*), another one from '*Cinchona henleana* woods' (*Steyermark 55097*). At elevations of 1100–1800 m. Flowering: June, July, August, December; fruiting: March, June, July, October.

Vernacular names — Not recorded.

Field observations — Ripe flowers have a scent of bananas when ripe.

Note — *Guatteria venezuelana* is quite distinctive by small, coriaceous leaves, an indument of erect, brown, mostly curly hairs on most vegetative parts, and shortly stipitate monocarps. In the last feature and in its small leaves it matches *G. schomburgkiana* fairly well, but that species has very short pedicels, while in *G. venezuelana* these are much longer.

169. *Guatteria venosa* Erkens & Maas — Map 37

Guatteria venosa Erkens & Maas in Erkens et al. (2008) 509, f. 18; Maas & Westra (2011) 141. — 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–)10–30 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, 16–48 by 6–16 cm (leaf index 2.6–3.6), coriaceous, not verruculose or sparsely to rather densely verruculose towards 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 towards the base, becoming sparsely verruculose to smooth towards the apex, secondary veins distinct, 25–35 on either side of primary vein, strongly impressed above, forming a marginal vein, at a smallest distance of 2–5 mm from the margin, tertiary veins slightly raised above, the major ones percurrent, the minor ones reticulate. *Flowers* in 1–2–several-flowered inflorescences mostly on branchlets just after leaf fall or on leafless branchlets; pedicels 10–20 mm long, 1.5–2 mm diam, fruiting pedicels to c. 25 mm long, c. 5 mm diam, densely covered with appressed hairs, articulated at 0.2–0.3 from the base, bracts c. 5, soon falling, not seen; flower buds depressed ovoid; sepals basally connate or free, broadly ovate-triangular, 5–6 by 5–6 mm, appressed to spreading, outer side densely covered with appressed hairs; petals green, greenish cream, brownish, or 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 papillate, hairy, to glabrous. *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, rugulose, raphe not distinct from rest of seed.

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

Fig. 84 *Guatteria venezuelana* R.E.Fr. Flowering branch (*Van der Werff 3624*, U).

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

Vernacular names — Ecuador: Cargadera negra (*Méndez et al. 284*, *Ortiz et al. 767*), Degteiug, Tilalde (Awapit) (*C. Aulestia & Grijalva 1187*), Guasca negra (*Thomsen 58834*).

Note — *Guatteria venosa* can be recognized by the high number of secondary veins (25–35 on each side of the primary vein) as compared to *Guatteria* species in general with the total number mostly about 20 or lower. Further distinctive features are the marginal vein, the verruculae (albeit relatively few) on the leaves, and the short stipes of the monocarps, all placing it in Fries's sect. *Mecocarpus* (Maas & Westra 2011).

170. *Guatteria verrucosa* R.E.Fr. — Plate 8h; Map 34

Guatteria verrucosa R.E.Fr. (1939) 519, f. 35a. — Type: *Brenes 4058* (holo F; iso F), Costa Rica, Alajuela, La Palma de San Ramón, 1175 m, 4 Sept. 1924.

Tree 3–28 m tall, to c. 50 cm diam; young twigs rather densely covered with appressed hairs or glabrous. *Leaves*: petiole 3–5(–8) mm long, 1–2 mm diam; lamina narrowly elliptic to elliptic, 7–17 by 2.5–5 cm (leaf index 3–3.5), chartaceous, densely verruculose, dull, greyish green to brown above, brown below, glabrous above, sparsely covered with minute appressed hairs below, base acute to attenuate, decurrent along petiole, apex acuminate (acumen 5–15 mm long), primary vein flat to slightly raised above, sparsely covered with erect hairs along the primary vein above, sparsely covered with appressed hairs below, secondary veins distinct, 8–16 on either side of primary vein, raised above, smallest distance between loops and margin 1–3 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 10–15 mm long, c. 1 mm diam, fruiting pedicels to c. 25 mm long, c. 3 mm diam, rather densely to sparsely covered with appressed hairs, articulated at c. 0.3 from the base, bracts 4–6, soon falling, not seen; flower buds depressed ovoid; sepals free, shallowly ovate-triangular, 3–4 by 5–6 mm, reflexed, outer side rather densely to sparsely covered with appressed hairs; petals yellowish green, cream or pale yellow in vivo, broadly ovate to ovate, 8–15 by 6–9 mm, rather densely to sparsely covered with appressed hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 15–25, green, red, to finally purplish black in vivo, black in sicco, ellipsoid to ovoid or broadly so, somewhat wrinkled, 10–17 by 9–13 mm, glabrous, apex rounded, wall 1–5 mm thick, stipes 2–5 by 1–3 mm. *Seed* ellipsoid, 9–13 by 6–11 mm, dark brown, rugose, raphe not distinct from rest of seed.

Distribution — Costa Rica.

Habitat & Ecology — In lower montane rain forest. At elevations of 900–1600 m. Flowering: January, May, July, August, December; fruiting: March, August, November, December.

Vernacular names — Not recorded.

Notes — *Guatteria verrucosa* is easily confused with *G. oliviformis*. However, it can be recognized by a combination of young twigs densely covered with appressed hairs, leaves that are verruculose, and shortly stipitate, almost ovoid, very thick-walled monocarps. Also, this species is only known from the Monteverde region (Puntarenas) and the mountains of La Palma de San Ramón (Alajuela) in Costa Rica.

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

171. *Guatteria verruculosa* R.E.Fr. — Fig. 70h, i, 85; Map 34

Guatteria verruculosa R.E.Fr. (1956) 434, pl. 1. — Type: *Fosberg 19126* (holo S; iso P, US 2 sheets), Colombia, Norte de Santander, Cordillera Oriental, hills E of Valegrá, S of Quebrada Valegrá, Con. Chucarima, Mun. Chitagá, 2000 m, 16 Nov. 1942.

Tree c. 6 m tall, diam not recorded; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 5–10 mm long, 2–3 mm diam; lamina narrowly elliptic to narrowly obovate, 13–28 by 5–12 cm (leaf index 2.3–3.3), chartaceous, densely and minutely scabridulous, dull, dark grey to greyish green above, green to brown below, glabrous above, sparsely covered with appressed hairs, but soon almost glabrous below, base acute to slightly attenuate, apex bluntly acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 12–16 on either side of primary vein, impressed above, smallest distance between loops and margin 2–5 mm, tertiary veins slightly raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 10–25 mm long, 1–2 mm diam, fruiting pedicels to c. 3 mm diam, densely to rather densely covered with appressed hairs, articulated at 0.2–0.3 from the base, bracts 5–6, soon falling, not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–6 by 4–6 mm, appressed, outer side densely covered with appressed hairs; petals yellowish green in vivo, elliptic to oblong-elliptic or narrowly so, 10–20 by 3–8 mm, outer side densely covered with appressed hairs; stamens c. 2 mm long, connective shield papillate to glabrous. *Monocarps* 10–25, colour in vivo not recorded, black to brown in sicco, ellipsoid, 15–18 by 7–8 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 1 mm long), wall 0.5–0.8 mm thick, stipes 2–3 by c. 3 mm. *Seed* ellipsoid, 13–17 by 7–8 mm, brown, transversely and longitudinally grooved, raphe not distinct from rest of seed.

Distribution — Colombia (Norte de Santander), Venezuela (Barinas, Trujillo).

Habitat & Ecology — In non-inundated ('tall forest on gently sloping ground', 'selva') forest or on steep forest slopes along stream. At elevations of 850–2000 m. Flowering: February, June, November; fruiting: November.

Vernacular names — Not recorded.

Notes — *Guatteria verruculosa*, only known from the type collection, can be recognized by its scabridulous leaves. Other features are the very short stipes (to c. 3 mm long), the relatively thick monocarp wall and the very distinct secondary veins.

Guatteria verruculosa was placed by Fries (1956) in sect. *Chasmantha* and he compared it with *G. slateri*. It was, surprisingly, not included in the revision of sect. *Chasmantha* by Sánchez S. (1986).

172. *Guatteria villosissima* A.St.-Hil. — Fig. 86; Map 34

Guatteria villosissima A.St.-Hil. (1825) 38; R.E.Fr. (1939) 349. — *Cananga villosissima* (A.St.-Hil.) Warm. (1873) 144. — Type: *A.F.C.P de Saint-Hilaire 606* (holo P; iso P), Brazil, Minas Gerais, Rio Piracicaba, Serra dos Pilões ('près Itajuru de São Miguel de Mato Dentro'), Jan. 1817.

Guatteria villosissima A.St.-Hil. var. *longepedunculata* R.E.Fr. (1939) 351. — Type: *Dusén 1910* (holo S; iso LE, U), Brazil, Rio de Janeiro, Nova Friburgo, 22 Feb. 1903.

Tree or shrub 3–10 m tall, 3–8 cm diam; young twigs densely covered with erect, long-persisting hairs. *Leaves*: petiole 1–3 mm long, 2–3 mm diam; lamina narrowly elliptic to elliptic, 5–15 (–18) by 2–4 cm (leaf index 2.3–6), coriaceous to chartaceous, not verruculose, blackish green to brown above, pale brown below, sparsely covered with erect hairs above, densely covered with erect hairs below, margins revolute, base obtuse to cordate, apex acute, primary vein impressed above, secondary veins distinct, 10–15 on either side of primary vein, raised above, smallest distance between loops and margin 1–2 mm, tertiary veins raised above, reticulate. *Flowers* solitary in axils of leaves; pedicels 5–20 mm long, 1–3 mm diam, fruiting pedicels to c. 35 mm long, densely covered with erect, brown hairs, articulated at 0.2–0.5 from the base, bracts 5–7, mostly soon falling, the

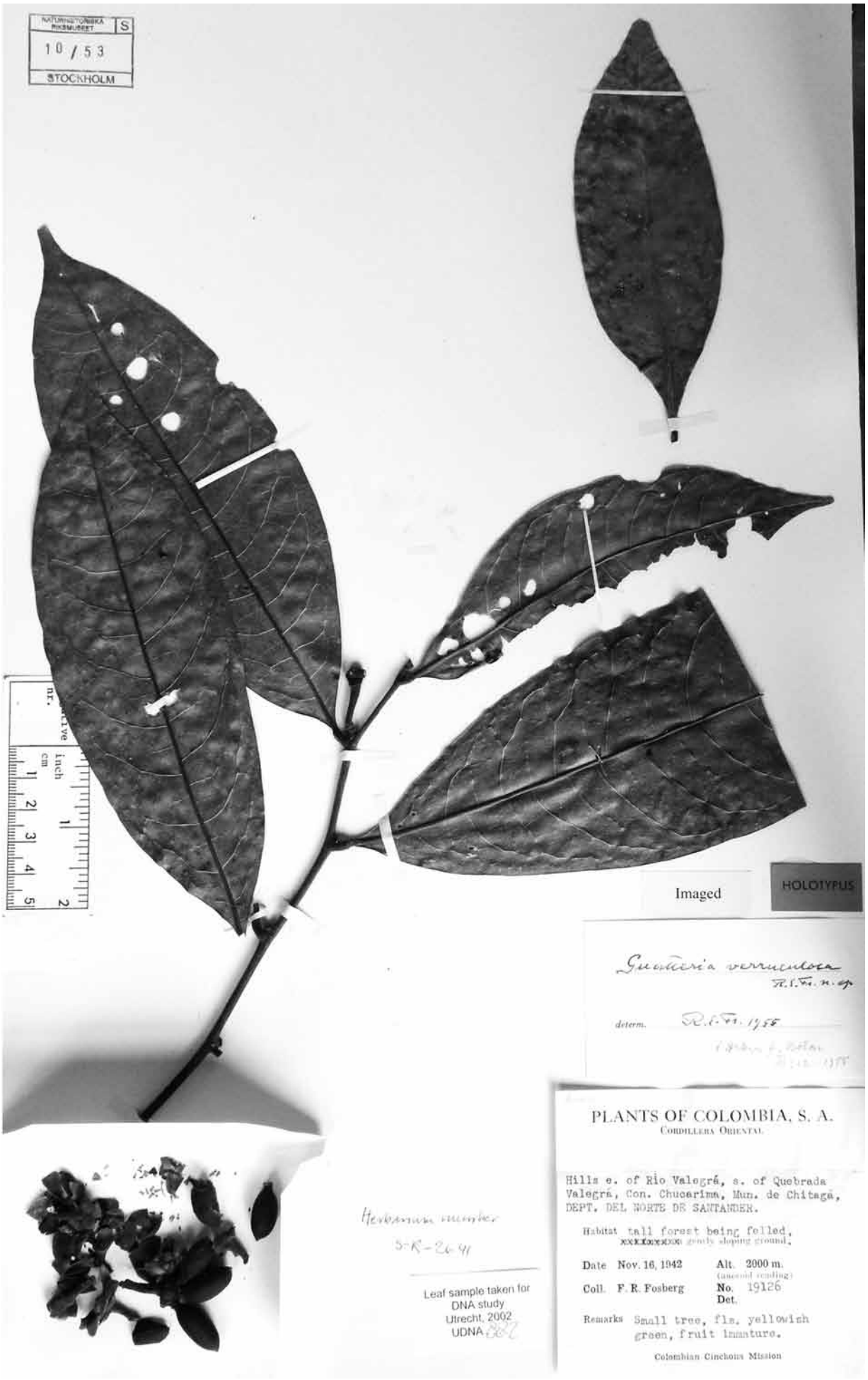


Fig. 85 *Guatteria verruculosa* R.E.Fr. Fertile branch (*Fosberg 19126*, holotype S).

Fig. 86 *Guatteria villosissima* A.St.-Hil. a. Flowering branch; b. fruit (a, b: *Pereira 2383*; from Lobão (2009) f. 12E, F).

uppermost bracts elliptic or sometimes narrowly elliptic, 7–15 mm long, lower bracts broadly elliptic, 1–4 mm long, rarely partly foliaceous, elliptic, c. 15 mm long; flower buds broadly ovoid; sepals free, but connate in bud, broadly ovate-triangular, 7–10 by 7 mm, appressed, outer side glabrous; petals green, reddish green, maturing yellow to red-orange in vivo, ovate to elliptic, 10–25 by 4–12 mm, outer side densely covered with erect, curly, brown hairs; stamens c. 1.5 mm long, connective shield papillate to glabrous. *Monocarps* 15–45, green, maturing purplish black in vivo, blackish in sicco, ellipsoid, 7–8 by 4–6 mm, sparsely covered with erect , brown hairs, soon glabrous, apex apiculate (apiculum c. 1 mm long), wall c. 0.3 mm thick, stipes 3–4 by 1 mm. *Seed* ellipsoid, c. 8 by 5–7 mm, brown, pitted, raphe raised.

Distribution — Brazil (Ceará, Espírito Santo, Minas Gerais, Rio de Janeiro).

Habitat & Ecology — In non-inundated, Atlantic rain forest, gallery forest or cerrado, on clayey to sandy soil. At elevations of 25–1800 m. Flowering: throughout the year; fruiting: throughout the year.

Vernacular names — Brazil: Pimenta-de-macaco (*Andrade & Lopes 5253*), Pindaíba ('Pindahyba') (*Mexia 4620*, *5277*).

Field observations — 'Flower's odor remembering fruits' (*Gottsberger 21-7774*).

Notes — *Guatteria villosissima* is characterized by almost sessile leaves, densely covered with erect hairs on the lower side, an obtuse to cordate leaf base, revolute leaf margins and by short stipes (3–4 mm long).

The species is quite similar to the widely distributed *G. tomentosa* (Central America and in many parts of tropical South America), differring by: obtuse vs pointed flower buds, leaf margins revolute all over its length vs basally revolute in *G. tomentosa*, and generally shorter stipes (3–4 vs 4–20 mm long).

Fig. 87 *Guatteria wachenheimii* Benoist. Fruiting branch (*Sabatier & Prévost 3951*, U).

Fig. 88 *Guatteria wachenheimii* Benoist. a. Fruit; b. flowers (a: *Sabatier & Prévost 3951*, U; b: *Sabatier & Prévost 3975*, U).

173. *Guatteria wachenheimii* Benoist — Fig. 87, 88a, b; Map 34

Guatteria wachenheimii Benoist (1927) 270; R.E.Fr. (1939) 484. — Type: *Wachenheim 201* (holo P; iso MO, P), French Guiana, Godebert, May 1920.
Guatteria microsperma R.E.Fr. (1957c) 236. — Type: *Cowan 38259* (holo S; iso NY, RB 2 sheets), Brazil, Amapá, Serra do Navio, Rio Amapari, N slopes of Observatorio Ore Body, 200 m, 11 Nov. 1954.

Tree 4–18 m tall, 2–50 cm diam; young twigs sparsely covered with erect hairs, soon glabrous. *Leaves*: petiole 4–9 mm long, 1–2 mm diam; lamina narrowly elliptic, 11–25 by 3–9 cm (leaf index 2.6–3.8), chartaceous, not verruculose, scabridulous, dull, grey to greyish green above, green to brown below, glabrous above and below, base acute, often distinctly attenuate, apex acuminate (acumen 5–20 mm long), primary vein impressed above, secondary veins distinct, 12–18 on either side of primary vein, impressed above, loop-forming at almost right angles and forming a marginal vein, at a smallest distance of 3–6 mm from the margin, tertiary veins inconspicuous or conspicuous, flat to slightly raised above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves or mostly on leafless branchlets, or plant cauliflorous; pedicels 10–25 mm long, 1–1.5 mm diam, fruiting pedicels to c. 2 mm diam, glabrous, articulated at 0.2–0.4 from the base, bracts 5–7, soon falling, basal ones very broadly or transversely elliptic, to c. 1 mm long, the upper ones not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 3–4 by 3–5 mm, appressed, outer side sparsely covered with appressed hairs, at the very margins and very apex densely so; petals green, maturing yellow in vivo, ovate, 11–20 by 6–8 mm, outer side densely covered with appressed hairs; stamens c. 2 mm long, connective shield hairy. *Monocarps* 20–40, deep red in vivo, brown or black in sicco, ellipsoid, 6–9 by 3–4 mm, glabrous, but sparsely covered with appressed hairs at base and apex, apex rounded to apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 2–6 by 0.5–1 mm. *Seed* ellipsoid or slightly obovoid, 6–8 by 3–4 mm, reddish brown, pitted and with few longitudinal grooves, raphe not distinct from rest of seed.

Distribution — Guyana, Suriname, French Guiana, Amazonian Brazil (Amapá).

Habitat & Ecology — In non-inundated forest, often on brown, lateritic soil. At elevations of 0–1000 m. Flowering: March to May, September; fruiting: January to March, August to December.

Vernacular names — Brazil: Envira-cheirosa (*N.A. Rosa 1040*). French Guiana: Mamayawé (Creole name). Suriname: Panta (Sranang name) (*Lindeman 5795*, *5892*).

Note — *Guatteria wachenheimii* is very easily recognizable by the scabridulous leaves which have a marginal vein and by its very small monocarps (hence the specific epithet for the synonymous *G. microcarpa*).

174. *Guatteria wokomungensis* Scharf & Maas — Map 34

Guatteria wokomungensis Scharf & Maas in Scharf et al. (2005) 570, f. 5. — Type: *Forest Department British Guiana 7941 = R. Boyan 117* (holo NY; iso FDG, K), Guyana, Mt Ayanganna, 2 Mar. 1960.

Tree 3–8 m tall, c. 10 cm diam; young twigs glabrous. *Leaves*: petiole 3–6 mm long, 1–2 mm diam; lamina narrowly elliptic, 9–15 by 4–6 cm (leaf index 2.3–3.5), coriaceous, not verruculose, dull, pale grey or lead grey above, yellowish or dark greenish brown below, glabrous on both sides, but young primary vein covered with a dense row of hairs, base acute to obtuse, slightly attenuate, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins distinct, 8–10 on either side of primary vein, raised above, loop-forming at right angles, forming a weak marginal vein, at a smallest distance of c. 2 mm from the margin, tertiary veins raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; flowering and fruiting pedicels 25–40 mm long, c. 1 mm diam, sparsely covered with erect hairs, articulated at 0.3–0.4 from the base, bracts 4–6, soon falling, not seen; flower buds broadly ovoid; sepals free, broadly ovate-triangular, 4–6 by 4–5 mm, appressed to spreading, outer side glabrous; petals green or greenish yellow in vivo, narrowly rhombic, 20–25 by 7–8 mm, outer side densely covered with erect, curly hairs; stamens c. 2 mm long, connective shield papillate, flat or slightly umbonate. *Monocarps* 8–20, green in vivo, dull black in sicco, ellipsoid, 10–12 by 6 mm, glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.2–0.3 mm thick, stipes 15–25 by c. 1 mm. *Seed* ellipsoid, c. 9 by 5 mm, dark brown, pitted, raphe raised.

Distribution — Guyana.

Habitat & Ecology — In mixed, non-inundated forest with Boba palms (*Socratea exorrhiza* (Mart.) H.Wendl.), *Euterpe* sp., *Clusia* sp., *Schefflera* sp. and *Licania* sp., between cliffs or mountain slopes, on peat, sandstone, grey sandy clay or red clay. At elevations of 915–1375 m. Flowering: March, June to August; fruiting: March.

Vernacular name — Guyana: Arara (Arawak name) (*Forest Department British Guiana 7941 = R. Boyan 117*).

Note — *Guatteria wokomungensis* is a species occurring in the mountains of W Guyana. It is recognizable by a low number of secondary veins and long pedicels (up to 40 mm long), which are sometimes provided with foliaceous bracts.

175. *Guatteria zamorae* Erkens & Maas — Map 34

Guatteria zamorae Erkens & Maas in Erkens et al. (2006) 213, t. 3, f. 6. — Type: *Maas et al. 9531* (holo U; iso INB, K, MO, NY, PMA, SCZ), Panama, Bocas del Toro, Canaza, road from Chiriquí Grande to David, 100 m, 29 May 2004.

Tree 10–15 m tall, to 30 cm diam; young twigs densely covered with erect, brown hairs, finally glabrous. *Leaves*: petiole 3–9 mm long, 1–2 mm diam; lamina narrowly obovate to narrowly elliptic, 10–18 by 3–5 cm (leaf index 3.3–3.6), chartaceous, densely to rather densely verruculose, dull, yellowish brown to greyish brown above, brown below, glabrous above, except for the densely hairy primary and sometimes secondary veins, densely to sparsely covered with erect, brown hairs below, base acute, apex acuminate (acumen 5–10 mm long), primary vein flat to slightly raised above, secondary veins distinct, 10–15 on either side of primary vein, raised above, smallest distance between loops and margin 2–3 mm, tertiary veins raised above, reticulate. *Flowers* in 1(–2)-flowered inflorescences in axils of leaves; pedicels 10–40 mm long, c. 1 mm diam, fruiting pedicels c. 2 mm diam, densely to rather densely covered with erect hairs, articulated at c. 0.3 from the base, bracts 5–6, soon falling, not seen; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 4–5 by 4–5 mm, spreading, extreme apex revolute, outer side rather densely to densely covered with appressed and erect hairs; petals green, greyish green or yellow in vivo, ovate to ovate-oblong, 10–15 by 5–8 mm, outer side densely covered with appressed and erect hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 30–50, green, maturing dark wine-red to black in vivo, black in sicco, ellipsoid, 9–12 by 4–5 mm, glabrous, except for some scattered hairs near the apex, apex apiculate (apiculum c. 1 mm long), wall 0.1–0.2 mm thick, stipes 6–10 by 1 mm. *Seed* narrowly ellipsoid, 8–10 by 3–4 mm, brown, transversely grooved to rugose, raphe impressed.

Distribution — Panama.

Habitat & Ecology — In forest and in pastures. At elevations of 100–700 m. Flowering: May; fruiting: May.

Vernacular names — Not recorded.

Note — *Guatteria zamorae* can be distinguished by an indument of erect hairs on the young leafy twigs, verrucose leaves, the yellowish brown leaf colour after drying, very small petals (10–15 mm long!) and relatively small leaves (10–18 by 3–5 cm).

176. *Guatteria sp. 1*

Tree 20–25 m tall, c. 45 cm diam; young twigs glabrous. *Leaves*: petiole 5–10 mm long, 1–1.5 mm diam; lamina narrowly elliptic, 11–16 by 4–5 cm (leaf index 2.2–3.5), chartaceous, not or weakly verruculose, shiny, brown to greyish brown above, brown to greyish below, glabrous above, sparsely covered with appressed hairs to glabrous below, base acute to attenuate, apex acuminate (acumen 5–10 mm long), primary vein impressed above, distinctly keeled or not below, secondary veins indistinct, 10–15 on either side of primary vein, slightly raised above, smallest distance between loops and margin 2–7 mm, tertiary veins slightly raised above, reticulate. *Flowers* only seen in fruiting stage, in 1–2-flowered inflorescences in axils of leaves; fruiting pedicels 6–20 mm long, 1.5–3 mm diam, glabrous, articulated at 0.3–0.5 from the base, bracts 5–6, soon falling, not seen. *Monocarps* 10–30, green, maturing black in vivo, black in sicco, ellipsoid, 10–13 by 5–6 mm, sparsely covered with appressed hairs, soon glabrous, apex apiculate (apiculum < 1 mm long), wall 0.1–0.3 mm thick, stipes 7–12 by 0.5–1 mm. *Seed* ellipsoid, 9–10 by 4–6 mm, brown, weakly pitted, raphe slightly raised or not distinct from rest of seed.

Distribution — Brazil (Amazonas, Pará).

Habitat & Ecology — In periodically inundated várzea forest. At elevations of about sea level. Flowering: unknown; fruiting: October.

Vernacular names — Not recorded.

Other specimens examined. Brazil, **Amazonas**, Rio Javarí, Tambaqui, 18 Oct. 1976, *Prance et al. 23894* (INPA, U). **Pará**, Ilha do Marajó, Rio Jipuru, 24 Oct. 1987, *Tavares et al. 266* (U).

Note — This material, restricted to várzea forests, posssibly represents an undescribed species, characterized by completely glabrous young twigs. As flower material is still lacking we refrained from naming it.

177. *Guatteria sp. 2*

Tree 10–12 m tall, 5–15 cm diam; young twigs densely covered with erect, brown hairs, soon glabrous. *Leaves*: petiole 4–10 mm long, 1–2 mm diam; lamina narrowly elliptic, 14–20 by 4–6.5 cm (leaf index 2.8–3.5), chartaceous, not verruculose, dull, greyish above, brown below, densely covered with appressed hairs to glabrous above, sparsely covered with appressed hairs to glabrous below, base acute to slightly attenuate, apex acuminate (acumen 5–15 mm long), primary vein impressed above, secondary veins distinct, 15–17 on either side of primary vein, slightly impressed above, smallest distance between loops and margin c. 2 mm, tertiary veins flat above, reticulate. *Flowers* in 1–2-flowered inflorescences in axils of leaves; pedicels 7–15 mm long, c. 1 mm diam, fruiting pedicels to c. 15 mm long, to c. 1 mm diam, densely covered with appressed and erect, brown hairs, articulated at c. 0.3 from the base, bracts not seen; flower buds subglobose; sepals free, broadly ovate-triangular, 7–8 by 6 mm, appressed, but apex reflexed, outer and inner side densely covered with appressed and erect, brown hairs, inner base glabrous; petals green in vivo, ovate-elliptic, 7–10 by 5–7 mm, both sides densely covered with appressed and erect, brown hairs, except for the inner glabrous base; stamens c. 1.5 mm long, connective shield papillate. *Monocarps* 8–10, colour in vivo not recorded, black in sicco, ellipsoid, 15–20 by 5 mm, glabrous, apex apiculate (apiculum < 0.5 mm long), wall not measured, stipes 15–20 by c. 5 mm. *Seed* not seen.

Distribution — Colombia (Meta, Vichada).

Habitat & Ecology — In forest (?). At elevations of 100–350 m. Flowering: January, February, April; fruiting: June.

Vernacular names — Not recorded.

Notes — *Guatteria sp. 2* was examined in several herbaria during a visit by the first author to Colomba in 2013, all specimens having been incorrectly named *G. ferruginea*, a species from SE Brazil. It is very well marked by a dense indument of erect and appressed, brown hairs on many parts of the plant. The petals, too, are also hairy on both sides, except for the completely glabrous inner base. Since Colombian Government regulations do not permit herbarium material to be sent abroad we were unable to complete the study properly through a formal description and designation of a type.

It involves the following collections: *Aldona & Stevenson 10* (ANDES, COL), *Cabrera R. 1991* (COL), *2522* (COL), *Correa-Gómez 87* (COL), *128* (COL), all from the state of Vichada and *Aldona & Stevenson 22* (ANDES, COL) from Meta.

EXCLUDED SPECIES

Guatteria apodocarpa Mart. (1841) 30. — Type: *Martius s.n.* (holo M) = ***Annona parviflora*** (A.St.-Hil.) H.Rainer.

Guatteria berteriana Spreng. (1825) 635. — Type: *Bertero s.n.* (holo TO) = ***Drypetes alba*** Poit. {*Putranjivaceae*}.

Guatteria bibracteata (Hook.) Hemsl. (1878) 1. — *Annona bibracteata* Hook. (1841) t. 328. — Type: *Galeotti 7083* (holo G) = ***Desmopsis trunciflora*** (Schltdl. & Cham.) G.E.Schatz.

Guatteria boyacana J.F.Macbr. (1918) 50. — Type: *Whitford & Pinzon 13* (holo GH; iso US) = ***Pseudomalmea boyacana*** (J.F.Macbr.) Chatrou.

Guatteria brevipes DC. in Dunal (1817) 126. — Type: *Martin s.n.* (holo G; iso BM, K, S) = ***Cremastosperma brevipes*** (DC.) R.E.Fr.

Guatteria cuspidata Rusby (1927) 245. — Type: *M. Cárdenas 1706* (holo NY) = ***Sorocea sprucei*** (Baill.) J.F.Macbr. subsp. ***sprucei*** {*Moraceae*}.

Guatteria depressa (Baill.) Saff. ex Standl. (1922) 278. — *Annona depressa* Baill. (1868b) 267. — *Malmea depressa* (Baill.) R.E.Fr. (1930) 43. — Type: *Liebmann 20* (holo C 2 sheets) = ***Mosannona depressa*** (Baill.) Chatrou subsp. ***depressa***.

Guatteria gaumeri Greenm. (1907) 251. — *Malmea gaumeri* (Greenm.) Lundell (1974) 27. — Type: *Gaumer 189160*, *189161*, *189976*, *189977* and *189978* (syn F) = ***Mosannona depressa*** (Baill.) Chatrou subsp. ***depressa***.

Guatteria hypoglauca Standl. (1929) 207. — *Malmea hypoglauca* (Standl.) R.E.Fr. (1931) 321. — Type: *Cooper 661* (holo F; iso US) = ***Mosannona hypoglauca*** (Standl.) Chatrou.

Guatteria laevigata Mart. (1841) 32. — Type: *Poeppig 2638* (holo W, destroyed in 1945; iso BR) = ***Pseudoxandra lucida*** R.E.Fr.

Guatteria laurifolia (Sw.) Dunal (1817) 132, t. 32. — *Uvaria laurifolia* Sw. (1800) 1001. — Type: *Swartz s.n.* (holo S) = ***Oxandra laurifolia*** (Sw.) A.Rich.

Guatteria leiophylla (Donn.Sm.) Saff. ex Standl. (1930) 268. — *Duguetia leiophylla* Donn.Sm. (1895) 281. — *Malmea leiophylla* (Donn.Sm.) Lundell (1974) 28. — Type: *Thieme 5129* (holo US 3 sheets) = ***Mosannona depressa*** (Baill.) Chatrou subsp. ***depressa***.

Guatteria lucida Rusby (1927) 245, non C. Presl. — *Guatteria rusbyi* J.F.Macbr. (1929) 171. — Type: *O.E. White 913* (holo NY) = ***Cremastosperma monospermum*** (Rusby) R.E.Fr.

Guatteria lutescens Pohl ex Mart. (1841) 24, nom. nud. = ***Duguetia pohliana*** Mart.

Guatteria macrantha C.Presl (1835) 78; R.E.Fr. (1939) 539; Erkens et al. (2008) 502, f. 13. — Type: *Haenke s.n.* (holo PR), locality unknown = ***Uvaria*** sp.

Guatteria magnifica Ruiz & Pav. ex G.Don (1831) 100. — Type: *H. Ruiz s.n.*, *anno 1800* (holo B) = ***Unonopsis magnifolia*** R.E.Fr.

Guatteria martiana Schltdl. (1834) 326. — Type: *Sellow B 1970*, *C 1483* (holo B) = ***Oxandra martiana*** (Schltdl.) R.E.Fr.

Guatteria multiflora Poepp. ex Baill. (1868a) 216, nom. nud. = ***Bocageopsis multiflora*** (Mart.) R.E.Fr.

Guatteria ovalis Ruiz & Pav. (1798) 146. — Type: *H.Ruiz & J.J.A. Pavón s.n.* (holo B; iso F, MA 5 sheets) = ***Ruizodendron ovale*** (Ruiz & Pav.) R.E.Fr.

Guatteria pachypetala (Diels) J.F.Macbr. (1929) 171. — *Oxandra pachypetala* Diels (1927) 173. — Type: *Tessmann 4893* (holo B) = ***Anaxagorea pachypetala*** (Diels) R.E.Fr.

Guatteria peduncularis (Steud.) Pulle (1907) 124. — *Annona peduncularis* Steud. (1843) 754. — Type: *Hostmann & Kappler 1116*, *ed. Hohenacker* = *Hostmann 1116* (holo P; iso BM, K, S, U) = ***Unonopsis guatterioides*** (A.DC.) R.E.Fr.

Guatteria pendula Ruiz & Pav. (1798) 146. — Type: *J.J.A. Pavón s.n.* (holo G) = ***Cremastosperma pendulum*** (Ruiz & Pav.) R.E.Fr.

Guatteria poiteaui Diels (1931) 74. — *Cremastosperma poiteaui* (Diels) R.E.Fr. (1931) 328. — Type: *Poiteau s.n.* (holo G; iso F) = ***Cremastosperma brevipes*** (DC.) R.E.Fr.

Guatteria ponderosa Rusby (1910) 504. — Type: *R.S. Williams 1479* (holo NY) = ***Porcelia ponderosa*** (Rusby) Rusby.

Guatteria prinoides Spreng. (1825) 635. — Type: *Bertero s.n.* (?TO) = ***Drypetes alba*** Poit. {*Putranjivaceae*} (fide R.E.Fr. (1939) 540).

Guatteria raimondii Diels (1931) 75. — *Malmea raimondii* (Diels) R.E.Fr. (1931) 320. — Type: *Raimondi 1974* (lecto B, selected by Chatrou 1998) = ***Mosannona raimondii*** (Diels) Chatrou.

Guatteria rusbyi J.F.Macbr. (1929) 171. — *Guatteria lucida* Rusby (1927) 245, non C.Presl. — Type: *O.E. White 913* (holo NY) = ***Cremastosperma monospermum*** (Rusby) R.E.Fr.

Guatteria schlechtendaliana auct. non Mart.: Glaz. (1905) 11. — *Porcelia goyazensis* R.E.Fr. (1930) 33, f. 4a, b. = ***Porcelia macrocarpa*** (Warm.) R.E.Fr.

Guatteria socialis J.F.Macbr. (1929) 171. — Type: *C. Schunke 395* (holo F) = ***Cremastosperma pedunculatum*** (Diels) R.E.Fr.

Guatteria umbilicata Dunal (1817) t. 33. — Type: *Forsyth s.n.* (holo G 2 sheets) = ***Unonopsis umbilicata*** (Dunal) R.E.Fr.

Guatteria veneficiorum Mart. (1841) 34. — Type: *von Martius s.n.* (holo M) = ***Unonopsis veneficiorum*** (Mart.) R.E.Fr.

Guatteria virgata (Sw.) Dunal (1817) t. 31, nom. illeg. — *Uvaria virgata* Sw. (1800) 999. — *Bocagea virgata* (Sw.) Benth. & Hook.f. (1862) 29. — *Oxandra virgata* (Sw.) A.Rich. (1845) 20. — Type: *Swartz s.n.* (holo S) = ***Oxandra lanceolata*** (Sw.) Baill.

Guatteria xalapensis Baill. ex R.E.Fr. (1930) 43, nom. nud. = ***Mosannona depressa*** (Baill.) Chatrou subsp. ***depressa***.

Guatteria xanthochlora Diels (1927) 169. — *Malmea xanthochlora* (Diels) R.E.Fr. (1930) 45, f. 5a. — Type: *Tessmann 4553* (holo B) = ***Mosannona xanthochlora*** (Diels) Chatrou.

INSUFFICIENTLY KNOWN SPECIES

1. *Guatteria decandra* Ruiz & Pav. ex G.Don (1831) 100; R.E.Fr. (1939) 536

This species was described by G.Don as follows: “leaves oblong, acuminated, smooth except the nerves; peduncles lateral; flowers decandrous. S. Native of Peru. Uvària decándra, Ruiz. et Pav. MSS. in herb. Lamb. (v.s.)”. “*Decandrous* Guatteria. Shrub.”

Thus far no material of this species could be traced, although we tried BM, CGE, M and OXF. As there are no species of *Guatteria* known at all with such a low number of stamens, we doubt if this species belongs in *Guatteria*.

2. *Guatteria (?) lucida* C.Presl (1835) 78; R.E.Fr. (1939) 536. — Type: *Haenke s. n.* (holo ? PR 192593), Peru ('Habitata in peruviae')

Although not marked with the name *Guatteria lucida* material annotated as *Guatteria nitida* Presl in the PR Herbarium matches the short description of this species quite well as to leaves and fruits: "foliis basi obtusis ... coriaceis ... pedunculis solitariis ... carpellis pyriformibus", and may well represent the type. The material is too scanty, however, to enable any definite conclusion.

3. *Guatteria pavonii* Ruiz & Pav. ex G.Don (1831) 100; R.E.Fr. (1939) 536

This species was described by G.Don as follows: "leaves oblong-lanceolate, smooth, long, acuminated; branches clothed with brown villi as well as the petioles and the 1-flowered solitary axillary peduncles. S. Native of Peru. Uvària longifòlia, Ruiz. et Pav. MSS. in herb. Lamb. (v.s.)". "*Pavon's* Guatteria. Shrub".

Type: Two specimens in the Geneva Herbarium marked '*Waria* sp. nova *longifolia* NE' and '*Uvaria longifolia* NE' and both with a blue typed label 'Nueva España.. Herb. Pavon' are considered by us to be 2 syntypes of *G. pavonii.*

The material in Geneva in our opinion was too scanty to permit more precise identification.

4. *Guatteria viridiflora* Ruiz & Pav. ex G.Don (1831) 100; R.E.Fr. (1939) 536

This species was described by G.Don as follows: "leaves oblong-lanceolate, coriaceous, smooth; flowers solitary, terminal. S. Native of Peru. Uvària viridiflora Ruiz. et Pav. MSS. in herb. Lamb. (v.s.)". "*Green-flowered Guatteria*. Tree."

Thusfar no material of this species could be traced.

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IDENTIFICATION LIST

The abbreviations behind the collection numbers refer to the taxa as listed on p. 18.

Abbott 996: blai; 19020: sp. indet. – Abreu 132: aust – Acevedo et al. 186: ampl; 187: ucay – Acevedo-R. et al. 1293: aeru aff.; 5863: oure; 5963: punc; 6071: sp. indet.; 6076: blep; 7355: scal; 7408: decu; 7750: blai; 8068: subs; 8076: hete; 8215: scho; 8266: hete; 8350: scyt; 8973: ucay; 9082: rami; 10268: ucay; 10325: lies; 10350: atab; 10400: lies; 12318: punc; 13591: disc – Ackermann s.n.: vill – Acosta 1121: sp. indet. – Acosta P. & Ceja 1654: ampl – Acosta Rojas et al. 19: punc; 1098: doli – Acosta V. et al. 155: ampl; 1159: doli; 1200: ampl; 1295: rost; 1397: ampl; 1446: ampl; 1503: chiri; 2411: oliv; 2438: ampl; 3606: aeru; 3652: ampl; 4143: ampl; 8202: doli – Acuña et al. s.n.: blai; 9822: blai; 12421: blai; 13100: blai; 23361: blai – Adalardo-Oliveira et al. 2713: subs – Agostini et al. 152: saff; 489: sp. indet.; 1108: saff – Agudelo et al. s.n.: ampl – Aguiar & Cavalcanti 433: aust – Aguilar, M. & Castro 1023: foli; 1030: foli – Aguilar, R. et al. 13: aeru; 83: sp. indet.; 235: ampl; 468: pudi; 567: pudi; 731: luce; 733: luce; 996: ampl; 1034: ampl; 1121: pacc; 1529: chiri; 1723: ampl; 2031: rein; 2478: ampl; 2618: pudi; 2640: ampl; 2737: doli; 2778: pudi; 3654: rost; 3746: luce; 4147: aeru; 4174: aeru; 4182: luce; 4275: ampl; 4453: tala; 4611: rost; 4787: rost; 4810: rein; 4833: ucay; 4855: sp. indet.; 4901: sp. indet.; 4932: sp. indet.; 4955: luce; 4958: sp. indet.; 5175: cost; 5252: aeru; 6558: ampl; 6823: chiri; 8206: ampl; 10680: luce; 10691: sp. indet.; 11163: ampl; 11544: ampl; 11555: pudi; 11560: pudi; 11563: pudi; 11659: luce; 13118: rost – Aguilar, S. et al. 503: sess; 575: alat; 672: sp. indet.; 970: ampl; 6905: aber – Aguinda et al. 280: guia; 541: ucay; 590: ucay; 1416: punc; 1588: punc – Aguirre 241: oliv – Aguirre G. et al. 44: punc; 1073: magu; 1130: ucay – Aizprúa et al. S 198: luce; B 1918: luce; B 2114: luce; S 2293: ampl; S 2395: luce; B 2489: ampl; 2586: slat; S 2640: ampl; B 2955: ampl; B 3179: dari; B 3375: aber; 3676: ampl; B 4240: pana – Aké Assi et al. 16308: cari – Alanes et al. 180: tome; 203: punc – Alarcón N. 19: sp. indet.; 20: disc – Alban 6942: rigi; 7186: scho – Albert E. et al. 1732: paci; 2226: punc; 3243: punc; 3270: pitt; 4600: goud; 4618: goud; 4622: goud; 4623: goud; 4663: goud; 4893: goud; 4936: goud; 4969: ucay; 5066: ucay; 5083: ucay; 5136: goud; 5210: ucay; 5212: goud; 5214: goud; 5221: goud; 5339: goud; 6300: ucay; 6538: goud; 6693: ucay; 6831: sp. indet.; 6841: ucay; 7165: ucay; 7458: goud; 7546: ucay; 7872: ucay; 8077: ucay; 8215: ucay; 8361: punc – Albuquerque, B.W.P. et al. 227: inun; 271: inun; 1341: beck – Albuquerque, J.E. 1835: aust; 1860: aust – Albuquerque, S.Z.

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LIST OF VERNACULAR NAMES

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Agua catillo (ampl)
Ahuabaca (scyt)
Amajo-preto (citr)
Amarillo (punc)
Anon (ucay)
Anona (aeru, alba, conf, flab, inun, megp)
Anona de montaña (aeru)
Anona de monte (hirs)
Annoncillo (punc, scho)
Anonilla [Anonillo] (blep, flab, foli, inun, megp, oliv, punc, revo)
Anonilla blanca (punc)
Anonilla-carahuasca (flab)
Apukutitei (scan)
Arara (punc, scho, woko)
Araraballi (scho)
Araticum (came, pohl)
Arbol de agua (megp)
Aremenango (scho)
Aremenango wéwé (scho)
Atzmiriqui (duod)
Auca hicoja (megp, punc, rami)
Baakakungè (scho)
Baaka pau, mamaai (punc)
Bako pao (pann)
Bara (inun, long, megp)
Baracaspi [Bar(r)a caspi] (inun, flab, megp)
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Black maho (punc, scho)
Black Yarri-Yarri (flex, scho)
Blaka paw (punc)
Boesi-soensaka (punc)
Bois nouè (cari)
Bois violin (cari)
Bosolijf (scan)
Boszuurzak (proc, punc, scho)
Burillo (chir)
Buruchicú [Buruchicu, Butruchicu, Buutruchicu] (arar, long, tric)
Busisunsaka (scho)
Cïbo dujecu (foli)
Cabo de pala (ucay)
Cacaia-velha (inun)
Cafesillo (carc)
Cambuí (aust)
Canalú (sess)
Candelero [Candilero] (graf)
Canguantã (lati)
Caracaspi [Cara caspi] (decu, megp, mode)
Carahuasca [Cara huasca] (decu, dura, elat, flab, gent, guia, hirs, inun, megp, meli, mode, punc, rami, revo, rubo, sanc, scyt, stip, ucay)
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Carahuasca blanca [Caruhuasca blanca] (flab, ucay)
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Cararasca (spec)
Caravasca (punc)
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Cargadero blanco (cuat, pitt)
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Cargadero negro (cuat, elet, punc)
Cargadero punta de lanza (cuat)
Cargamarillo (crap)
Carguero (arar, megp, scal)
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Cedrillo (cuat)
Chalviande (cuat)
Chaporoasca (mode)
Cherimoya (megp)
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Chinanim (stip)
Chirimoya del monte (punc)
Chiuanim [Chiwanim] (megp)
Chiwiachim (punc, rami)
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Envira-da-folha-grande (rami)
Envira-da-folha-peluda (tome)
Envira-da-mata (guia)
Envira-do-igapó (inun)
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Envira-fofa-da-folha-grande (ucay)
Envira-manga-de-anta (punc)
Envira-mole (scyt)
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Envira-rolinha (disc)
Envira-tambaqui (hirs)
Envireira (blep, disc, duck, frie, hisp, punc, scyt, ucay)
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Maguaná (saff)
Mahaut noir (cari)
Majagua [Mahagua] (citr, flex, foli, hete, inun, magu, mayp, megp, punc, subs, ucay)
Majagua anon (scho)
Majagua blanca (punc)
Majagua hoja grande (long)
Majagua hoja larga (punc)
Majagua negra (dura, inun, punc, scho, subs)
Majagua orillera (inun)
Majagua rebalsera (inun)
Majagua verde [Majagua verde] (foli, mayp, proc, punc, rubr, scho, scyt)
Majagüillo (scho)
Majaguillo montañero (rubr)
Majaguillo negro (ucay)
Malagueto (ampl, pudi)
Malagueto negro (ampl)
Malagueto prieto (slat)
Malakopesi (scan)
Maman yawée [Mamayavé, Mamanyaoué, Mamanyaoui, Mamanyaré, Mamayawé] (guia, inte, oure, punc, scho, wach)
Mamayawé commun (punc)
Maria-preta (citr)
Matau'i, (disc)
Maurel canelón (punc)
Mayoballi wadilikoro (scho)
Menedowe (chrys)
Midha dhahua (punc)
Millua hicoja (tome)
Minudawa (mode)
Miret (disc)
Moncapatamo (guia)
Motelo caspi (inun)
Mucataremon (punc)
Muecantokaro-riká (guia)
Mulewa [Moelewa, Moerewa] (scan)
Mulokju (scan)
Muraya (punc)
Ñaajeku (arar)
Ñaatraje dujeku (long)
Nagewe (scal)
Nagui (stip)
Naqueno (lies)
Ndulu ndulu (scan)
Neayatio (punc)
Negrillo (hirs)
Ñinchu (pitt)
Nuanamú (cuat)
Oitahumo (brev)
Olijf (scan)
Olijfrank (scan)
Olijfvrucht (scan)
Oñitahue [Oñetahue, Oñintahua, Oñitahua] (mode, punc, rami, stip, ucay)
Oñitahuemo (punc, rami, ucay)
Ouregou (oure)
Oyshobo (duod)
Palay (nari)
Palo de boya negro (hete)
Palo de buho (tric)
Palo de chombo (graf)
Palo de perfume (insc)
Palo de zope [Palo de zopo] (graf)
Palo pancho verde (punc)
Palo yais (past)
Pá-ma (ucay)
Panapualiki (scyt)
Pandiecou (pann)
Panta (punc, scho, wach)
Payuri-rang [Payuriran] (scho
Pegreku [Pegrekoe] (scho)
Pegrekupisi [Pedrekoe pisi, Pegrekoe-pisie] (punc, scho)
Peka (scho)
Pêpëêëpe uwii (scho)
Pêpëkusátu (scho)
Peprewiwiri [Pepe wiri] (scho)
Peseu (gale)
Pimenta-de-macao (vill)
Pimienta malagueta (blai)
Pina? ipinu (punc)
Pinaou (punc)
Pindaíba [Pindahyba] (aust, cand, macr, vill)
Pindaíba-cabo-de-rodo (olig)
Pindaíba-candoleana (cand)
Pindaíba-da/de-capoeira (cand)
Pindaíba-mole (cand)
Pindaíba-preta (blep)
Piraquina (duod, punc, scyt, tome)
Piraquina blanca (disc)
Piraquina de barbecho (punc, tome)
Piraquina macho (hirs)
Piraquina negra [Peraquina negra] (hirs, punc, scyt, ucay)
Piraquina peluda de barbecho (tome)
Pitaruguï (lies)
Pomme canelle (guia)
Pö-ö-ká-no (guia)
Pungaracaspi (scal)
Pungaramuyo (scal)
Punta de lanza (micr)
Puruna-do-nativo (cand)
Pweé-ka-no (guia)
Quïbojïdujecu (atab)
Quiyamas (ucay)
Raspadero (saff)
Rayado (paci)
Runa caspi (mode)
Sacha aguaja (megp)
Sangro blanco (aeru)

Savanne pegreku [Savannepedreku] (scho)
Seiseiunahi (punc)
Shapattovo (punc)
Sigui war (luce)
Small kind Arara (scho)
Smooth skin Arara (palu, proc, scho)
Suta (hirs)
Tairu (ucay)
Taiwi'i (punc)
Tata'y (scan)
Tetalde (pitt)
Ti-cachiman-bois (cari)
Tintuk (megp)
Tortuga (blep)
Tortuga caspi (megp)
Ucucha anona (punc)
Uñitahue [Uñetahue, Uñitawe] (lies, mode, scal)
Upupede (scan)
Vara (megp)
Vara blanca (dura)
Verdecito (ucay)
Wampu yais [Wampuyais, Wámpuyais, Wámpu yéis] (mode, past, punc, ucay)
Wanegu (scan)
Washi yais [Wáshi yéis, Wasri yais, Wuáshi yais] (guia, megp)
Wild soursop (cari)
Wime etni kamwi (scan)
Wosewayek (punc)
Xahui (scyt)
Yais [Yaïs] (decu, megp, mode, past, punc, stip, ucay)
Yam yais (mode)
Yana baru (megp)
Yana huasca (punc)
Yarayara (punc)
Yarayara amarilla (punc)
Yarayara morada (flex, punc)
Yaris (guia)
Yariyari (cons)
Yaroyaro (scho)
Yaya (blai)
Yaya blanca (dari)
Yaya fancesa (blai)
Yayo (aber)
Yeis (mode)
Yoarno (scan)
Yumi yeis (mode, stip, ucay)
Zopo (graf)
Zorro caspi [Zoro caspi] (meli, punc, scyt)
Zuto (punc)

APPENDIX

INDEX TO PALAEOTROPICAL NAMES OF GUATTERIA

(I.A. Turner, Royal Botanic Gardens Kew, Richmond, Surrey TR9 3AE, UK)

[*Guatteria acuminata* Lignur & Bey, Bull. Soc. Linn. Normandie sér. 5 5: 168. 1901, nom. nud.]
= ?***Monoon acuminatum*** (Thwaites) B.Xue & R.M.K. Saunders, Taxon 61: 1030. 2012.

Guatteria acutifolia Dunal, Monogr. Anonac. 134, 1817. Lecto (designated by Turner in press): Rheede, Hort. Malab. 5: t. 18. 1685.
= ***Huberantha korinti*** (Dunal) Chaowasku in Chaowasku et al., Kew Bull. 70: 23. 2015.

Guatteria bemban Miq., Fl. Ned. Ind., Eerste Bijv. 377. 1860. Lecto (designated here): Sumatra, Palembang, Moeara doewa, [*J. E. Teijsmann s.n.*] H.B. 3895 (U (barcode no. U0000364)).
≡ ***Monoon bemban*** (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 2: 45. 1865.

Guatteria bifaria A.DC., Mem. Soc. Phys. Genève 5: 217. 1832. Lecto (designated by Turner (Phytotaxa 32: 46. 2011): Burma, Prome, September–October 1826, *N. Wallich s.n.* [EIC 6447] (lecto K-W; isolecto CAL).
= ***Huberantha cerasoides*** (Roxb.) Chaowasku in Chaowasku et al., Kew Bull. 70: 23. 2015.

Guatteria biglandulosa Blume, Fl. Javae Anon. 102. t. 51. 1830. Type: Indonesia, Java: in montibus provinciae Bantam (?Spanoghe collection).
≡ ***Friesodielsia biglandulosa*** (Blume) Steenis, Blumea 12: 358. 1964.

Guatteria bragma Blume, Bijdr. 20. 1825. Lecto, designated by Van Heusden, Nordic J. Bot. 17: 175. 1996: Indonesia, Java, *C.L. Blume 1713* (lecto L (barcode no. L 0038206), isolecto K).
= ***Trivalvaria macrophylla*** (Blume) Miq., Ann. Mus. Bot. Lugduno-Batavi 2: 19. 1865.

Guatteria brevipetala Miq., Fl. Ned. Ind., Eerste Bijv. 381. 1861. Lecto (designated by Van Heusden, Nordic J. Bot. 17: 175. 1996): Indonesia, Sumatra, Poeloe Pisang, Padang, *Anon. s.n.* [Herb. Bogor. no. 497] (lecto U (barcodeno. U 0000421)).
= ***Trivalvaria macrophylla*** (Blume) Miq., Ann. Mus. Bot. Lugduno-Batavi 2: 19. 1865.

Guatteria canangioides Rchb.f. & Zoll., Linnaea 29: 323. 1857. Lecto (designated by Turner, Phytotaxa 36: 78. 2011): Indonesia, Sumatra, province of Lampong, *H. Zollinger 3047* (P (barcode no. P01983362); isolecto ?BM, ?P).
= ***Huberantha rumphii*** (Blume ex Hensch.) Chaowasku in Chaowasku et al., Kew Bull. 70: 23. 2015.

[*Guatteria caudata* Wall, Numer. List 6452. 1832, nom. nud.]
≡ ***Xylopia caudata*** Hook.f. & Thomson, Fl. Ind. 125. 1855.

Guatteria cerasoides (Roxb.) Dunal, Monogr. Anonac. 127. 1817. Basionym: Uvaria cerasoides Roxb., Pl. Coromandel 1: 30. t. 33. 1795. Lecto (designated by Huber, Rev. Handb. Fl. Ceylon 5: 35. 1985): Roxburgh, Pl. Coromandel 1: t. 33. 1795.
≡ ***Huberantha cerasoides*** (Roxb.) Chaowasku in Chaowasku et al., Kew Bull. 70: 23. 2015.

[*Guatteria cinnamomea* Wall., Numer. List. 6444. 1832, nom. nud.]
≡ ***Polyalthia cinnamomea*** Hook. f. & Thomson, Fl. Ind. 138. 1855.

[*Guatteria cinnamomea* Hook.f. & Thomson, Fl. Ind. 1: 138. 1855, nom. inval.]
≡ ***Polyalthia cinnamomea*** Hook.f. & Thomson

Guatteria coffeoides Thwaites ex Hook.f. & Thomson, Fl. Ind. 1: 141. 1855. Lecto (designated by Turner in press): Ceylon [Sri Lanka], C. P. 2503 (lecto K (barcode no. K000691485)).
≡ ***Monoon coffeoides*** (Thwaites) B.Xue & R.M.K.Saunders, Taxon 61: 1030. 2012.

Guatteria cordata Dunal, Monogr. Anonac. 129. t. 30. 1817 ≡ *Uvaria cordata* (Dunal) Wall. ex Alston, Handbook Fl. Ceylon 6 suppl.: 4. 1931, nom. illegit., non U. cordata Schumach. & Thonn. (1827). Lecto (designated by Turner in press): Dunal, Monogr. Anon. t. 30. 1817.
= ***Uvaria littoralis*** (Blume) Blume, Fl. Javae Anon. 26. 1830.

Guatteria costata Hook.f. & Thomson, Fl. Ind. 1: 143. 1855. Type: Burma, Needaun (Nidaun), 28 January 1827, *N. Wallich 1280* [EIC 6480] (holo K-W).
≡ ***Trivalvaria costata*** (Hook.f. & Thomson) I.M.Turner, Kew Bull. 64: 577. 2009.

Guatteria cuneiformis Blume, Bijdr. 19. 1825. Lecto (designated here): Java, [?in monte Salak], *C.L. Blume s.n.* (lecto L (barcode no. L0037939)).
≡ ***Friesodielsia cuneiformis*** (Blume) Steenis, Blumea 12: 358. 1964.

Guatteria eriantha Rchb.f. & Zoll., Linnaea 29: 323. 1858. Type: Java, *Zollinger 1714* (not traced).
= ?***Polyalthia*** sp.

Guatteria eupoda Miq., Fl. Ned. Ind., Eerste Bijv. 380. 1861. Lecto (designated here): Sumatra, Province of Tobing, [*F.W. Junghuhn s.n.*] (lecto U (barcode no. U0000366)).
≡ ***Miliusa eupoda*** (Miq.) I.M.Turner, comb. nov.

[*Guatteria fasciculata* Wall., Report, by N. Wallich, on the Royal Botanic Garden, Calcutta 15. 1840.]
= ***Monoon simiarum*** (Benth. & Hook.f.) B.Xue & R.M.K. Saunders, Taxon 61: 1033. 2012.

Guatteria fragrans Dalzell, Hooker's J. Bot. Kew Gard. Misc. 3: 206. 1851. Lecto (designated by Turner in press): [India], *N.A. Dalzell s.n.* (lecto K (barcode no. K000691484)).
≡ ***Monoon fragrans*** (Dalzell) B.Xue & R.M.K.Saunders, Taxon 61: 1031. 2012.

Guatteria glauca (Hassk.) Miq., Fl. Ned. Ind. 1(2): 49. 1858, nom. illegit., non G. glauca Ruiz & Pavón (1798). Basionym: *Uvaria glauca* Hassk., Flora (Beiblätt.) 25, 2(2): 31. 1842. Lecto (designated by Turner, Phytotaxa 36: 46. 2011): Indonesia, Java: *J.K. Hasskarl s.n.* (lecto L (barcode no. L 0188666)).
≡ ***Maasia glauca*** (Hassk.) Mols et al., Syst. Bot. 33: 493. 2008.

Guatteria globosa A.DC., Mem. Soc. Phys. Genève 5: 217. 1832. Lecto (designated by Panigrahi & Mishra, Taxon 33: 713. 1984): Burma, Tavoy, 15 Oct. 1827, *W. Gomez 428* [EIC 6448] (lecto K-W; isolecto G).
≡ ***Miliusa globosa*** (A.DC.) Panigrahi & S.C.Mishra, Taxon 33: 713. 1984.

Guatteria hypoleuca Miq., Fl. Ned. Ind., Eerste Bijv. 381. 1861. Lecto (designated by Turner, Phytotaxa 36: 46. 2011): Indonesia, Java: *J.K. Hasskarl s.n.* (lecto L (barcode no. L 0188666)). Epitype (designated by Turner, Phytotaxa 36: 46. 2011): Indonesia, Java: Udjung Kulon Reserve, Mt Pajung, 17 Nov. 1960, A.J.G.H. Kostermans et al. UNESCO 165 (epitype L (barcode no. L 0188665); isoepitypes A, BO, G, K).
= ***Maasia glauca*** (Hassk.) Mols et al., Syst. Bot. 33: 493. 2008.

Guatteria imbricata Blume, Fl. Javae Anon. 94, t. 46, 52C. 1830. Lecto (designated by Saunders, Bot. J. Linn. Soc. 139: 234. 2002): Java, *C.L. Blume s.n.*, s.dat (lecto L (sheet no. 898.61-15); iso BM, Lx2).
= ***Goniothalamus costulatus*** Miq., Fl. Ned. Ind., Eerste Bijv. 3: 372. 1861

Guatteria incerta Blume, Fl. Javae Anon. 100. t. 49B. 1830. Lecto (designated by Van der Meijden, Leiden Bot. Ser. 7: 99. 1982): *Van Hasselt s.n.* (lecto L (sheet no. 908.171-1694)).
≡ ***Xanthophyllum incertum*** (Blume) Meijden, Leiden Bot. Ser. 7: 99 (1982) [*Polygalaceae*]

Guatteria jenkinsii Hook.f. & Thomson, Fl. Ind. 1: 141. 1855. Lecto (designated by Turner, Phytotaxa 36: 73. 2011): India, Assam, s.dat., *F. Jenkins s.n.* (lecto K (barcode no. K000691481)).
≡ ***Huberantha jenkinsii*** (Hook.f. & Thomson) Chaowasku in Chaowasku et al., Kew Bull. 70: 23. 2015.

Guatteria korinti Dunal, Monogr. Anonac. 133. 1817. Lecto (designated by Huber, Rev. Handb. Fl. Ceylon 5: 36. 1985): Rheede, Hort. Malab. 5: t. 14. 1685.
≡ ***Huberantha korinti*** (Dunal) Chaowasku in Chaowasku et al., Kew Bull. 70: 23. 2015.

Guatteria lateriflora Blume, Bijdr. 20. 1825. Lecto (designated by Turner, Phytotaxa 36: 74. 2011): Indonesia, Java: s.dat., *Anon. s.n.* (lecto L (barcode no. L 0188880)).
≡ ***Monoon lateriflorum*** (Blume) Miq., Ann. Mus. Bot. Lugd.-Bat. 2: 19. 1865.

Guatteria laurifolia J.Graham, Cat. Bomb. 4. 1839, nom. illegit., non *G. laurifolia* (Sw.) Dunal, Monogr. Anonac. 132. 1817. Neotype (designated by Turner in press): India, Concan, s.dat., *Stocks s.n.* (K).
= ***Sageraea laurina*** Dalzell, Hooker's J. Bot. Kew Gard. Misc. 3: 207. 1851.

Guatteria littoralis Blume, Fl. Javae Anon. 99. t. 49A. 1830.
≡ ***Marsypopetalum littorale*** (Blume) B.Xue & R.M.K. Saunders, Syst. Biodivers. 9, 1: 24. 2011.

Guatteria longifolia (Sonn.) Wall., *Numer. List 6442*. 1832. Basionym: *Uvaria longifolia* Sonn., Voy. Indes Orient. 2: 233, pl. 131. 1782. Voy. Indes Orient. (octavo ed.) 3: 260. 1782. Lecto (designated by Huber, Rev. Handb. Fl. Ceylon 5: 33. 1985): Sonnerat's plate in Voy. Indes Orient. 2: pl. 131. 1782.
≡ ***Monoon longifolium*** (Sonn.) B.Xue & R.M.K.Saunders, Taxon 61: 1032. 2012.

Guatteria macrantha C. Presl, Reliq. Haenk. 2: 78. 1831. Type: T. P. X. Haenke s.n. (holo PR).
= ?***Uvaria grandiflora*** Roxb. ex Hornem., Suppl. Hort. Bot. Hafn. 141. 1819.

Guatteria macrophylla A.DC., Mem. Soc. Phys. Genève 5: 218. 1832, nom. illegit., non *G. macrophylla* Blume, Bijdr. 19. 1825. Lecto (designated by Turner, Phytotaxa 32: 46. 2011): Burma, Tavoy, 22 October 1827, W. Gomez 459 [N. Wallich 2046, EIC 6451] (lecto K-W).
= ***Goniothalamus sesquipedalis*** (Colebr.) Hook. f. & Thomson, Fl. Ind. 108. 1855.

Guatteria macrophylla Blume, Bijdr. 19. 1825. Lecto (designated by Van Heusden, Nordic J. Bot. 17: 175. 1997). *C.L. Blume 1026* (lecto: L (barcode no. L0038204), isolecto L, P).
≡ ***Trivalvaria macrophylla*** (Blume) Miq., Ann. Mus. Bot. Lugd.-Bat. 2: 19. 1865.

Guatteria macrophylla var. *bragma* (Blume) Blume, Fl. Javae Anon. 97. 1830. Basionym: *Guatteria bragma* Blume, Bijdr. 20. 1825. Lecto, designated by Van Heusden, Nordic J. Bot. 17: 175. 1996: Indonesia, Java, *C.L. Blume 1713* (lecto L (barcode no. L 0038206); isolecto K).
= ***Trivalvaria macrophylla*** (Blume) Miq.

Guatteria macrophylla var. *glabrata* Blume, Fl. Javae Anonac. 97. 1830. Lecto (designated by Van Heusden, Nordic J. Bot. 17: 175. 1997): Java, *J.C.A. van Hasselt s.n.* (lecto L (barcode no. L0038207)).
≡ ***Trivalvaria macrophylla*** (Blume) Miq., Ann. Mus. Bot. Lugduno-Batavi 2: 19. 1865.

Guatteria macropoda (Miq.) Zipp. ex Burck, Nova Guinea 8: 429. 1911. Basionym: *Monoon macropodum* Miq., Ann. Mus. Bot. Lugd.-Bat. 2: 17. 1865. Lecto (designated by Mols & Keßler, Blumea 45: 219. 2000): Indonesia, Papua, West New Guinea, *A. Zippelius 191* (lecto L (barcode no. L 0046168); isolecto A, L).
= ***Phaeanthus ophthalmicus*** (Roxb. ex G.Don) J.Sinclair, Gard. Bull. Singapore 14: 374. 1955.

Guatteria malabarica Dunal, Monogr. Anon. 134. 1817. Lecto (designated by Turner in press): Rheede, Hort. Malab. 5: t. 17. 1685.
= ***Uvaria zeylanica*** L., Sp. Pl. 536. 1753.

Guatteria membranacea A.DC., Mem. Soc. Phys. Genève 5: 217. 1832. Lecto (designated by Turner, Phytotaxa 32: 46. 2011): Burma, Tavoy, 7 Dec. 1827, *W. Gomez 574* [N. Wallich 2024, EIC 6439] (lecto K-W; isolecto BM (barcode no. BM000636921)).
≡ ***Monoon nitidum*** (A.DC.) I.M.Turner, comb. nov. in press

Guatteria micrantha A.DC., Mém. Soc. Phys. Genève 5: 218. 1832. Lecto (designated by Utteridge, Blumea 45: 388. 2000): Burma, Martaban, Amherst, 17 June 1827, *W. Gomez 15* [N. Wallich 1287, EIC 6449] (lecto K-W; isolecto BM (barcode no. 000020774(BM)), G).
≡ ***Uvaria micrantha*** (A.DC.) Hook.f. & Thomson, Fl. Ind. 103. 1855.

Guatteria montana A.DC., Syst. Nat. 1: 508. 1818, nom. illegit., superfl. Based on the same type as G. malabarica Dunal
= ***Uvaria zeylanica*** L., Sp. Pl. 536. 1753.

[*Guatteria multinervis* Wall., Numer. List 6445. 1832, nom. nud.]
= ***Polyalthia motleyana*** (Hook.f.) Airy Shaw, Bull. Misc. Inform. 1939: 280. 1939.

Guatteria nitida A.DC., Mem. Soc. Phys. Genève 5: 217. 1832. Lecto (designated by Turner, Phytotaxa 32: 46. 2011): Burma, Tavoy, 7 Dec. 1827, *W. Gomez 574* [N. Wallich 2024, EIC 6439] (lecto K-W; isolecto BM (barcode no. BM000636921)).
≡ ***Monoon nitidum*** (A.DC.) I.M.Turner, comb. nov. in press

Guatteria oxycarpa Miq., Fl. Ned. Ind. 1(1): 49. 1859, nom. illegit., non *G. oxycarpa* Poepp. ex Mart., Fl. Bras. (Martius) 13(1): 38. 1841. Type: Indonesia, Sumatra, Priaman, s.dat., *J.E. Teijsmann s.n.* [Herb. Bogor. no. 503] (holo U).
≡ ***Goniothalamus giganteus*** Hook.f. & Thomson, Fl. Ind. 109. 1855.

Guatteria palembanica Miq., Fl. Ned. Ind., Eerste Bijv. 379. 1861. Type: Indonesia, Sumatra, Palembang, Moeara Doewa, s.dat., *J.E. Teijsmann s.n.* [Herb. Bogor. 3597] (holo U (barcode no. U 0000374)).
= ***Polyalthia cauliflora*** Hook.f. & Thomson, Fl. Ind. 138. 1855.

Guatteria pallida Blume, Bijdr. 20. 1825. Lecto (designated by Turner, Phytotaxa 36: 47. 2011): Indonesia, Java, s. dat., Anon. s.n. [?C.L. Blume] (L (barcode no. L0037981)).
≡ ***Marsypopetalum pallidum*** (Blume) Backer, Schoolfl. Java 36. 1911.

Guatteria pallida Hook.f. & Thomson, Fl. Ind. 1: 143. 1855, nom. illeg. non *G. pallida* Blume, Bijdr. 20. 1825. Lecto (designated by Mitra, Fasc. Fl. India 10: 10. 1982): Bangladesh, Sylhet, Sept. 1850, *J.D. Hooker & T. Thomson s.n.* (lecto K; isolecto A, P).
≡ ***Trivalvaria argentea*** (Hook.f. & Thomson) J.Sinclair, Sarawak Mus. J. 5: 603. 1951.

Guatteria parveana Miq., Fl. Ned. Ind. 1(2): 48. 1858. Type: Based on manuscript description by H. Zollinger of *Uvaria parveana*.
= ***Huberantha rumphii*** (Blume ex Hensch.) Chaowasku, Kew Bull. 70: 23. 2015.

Guatteria persicifolia Hook.f. & Thomson, Fl. Ind. 1: 140. 1855 ('*persicaefolia*'). Type: Ceylon [Sri Lanka], Narawelle, *J.G. Champion s.n.* (holo K (barcode no. K000691473)).
≡ ***Polyalthia persicifolia*** (Hook.f. & Thomson) Hook.f. & Thomson, Fl. Brit. India 1: 66. 1872.

Guatteria pilosa G.Don, Gen. Hist. 1: 100. 1831. Lecto (designated by Veldkamp, Gard. Bull. Singapore 62: 304. 2011: Indonesia, ?Moluccas, *W. Roxburgh s.n.* [EIC Herb. 6458A] (lecto K-W (barcode no. K000442826)).
= ***Uvaria hirsuta*** Jack, Malayan Misc. 1, 5: 46. 1820.

Guatteria pisocarpa Blume, Bijdr. 21. 1825. Lecto (designated by Ganesan in Turner, Phytotaxa 36: 84. 2011): Indonesia, Java, Gunung Parang, *C.L. Blume s.n.* ['1247'] (lecto L (barcode no. L 0190172), isolecto L (barcode no. L 0190174)).
≡ ***Popowia pisocarpa*** (Blume) Endl. ex Walp., Repert. Bot. Syst. 1: 74. 1842.

Guatteria pondok Miq. Fl. Ned. Ind., Eerste Bijv. 380. 1861. Type: Sumatra, Priaman, *H. Diepenhorst s.n.* [H. B. 2211] (holo U (barcode no. U0006299)).
= ***Monoon lateriflorum*** (Blume) Miq., Ann. Mus. Bot. Lugd.-Bat. 2: 19. 1865.

[*Guatteria ramosissima* Wall., Numer. List 7294. 1832, nom. nud.]
= ***Popowia pisocarpa*** (Blume) Endl. ex Walp., Repert. Bot. Syst. 1: 74. 1842.

Guatteria rufa Dunal, Monogr. Anon. 129. t. 29. 1817. Lecto (designated by Turner in press): Indies, *F. Lahaye [Delahaye] s.n.* (lecto P-JU (Herb. Juss. catal. no. 10795 B; barcode no. P00662854)).
≡ ***Uvaria rufa*** (Dunal) Blume, Fl. Javae Anon. 19, t. 4. 1830.

Guatteria rumphii Blume ex Hensch., Vita Rumphii 153. 1833. Type: Indonesia, Ambon, Entirely based on Arbor nigra parvifolia of Rumphius (1743: 10, t. 4, f. 2, t. 5).
≡ ***Huberantha rumphii*** (Blume ex Hensch.) Chaowasku in Chaowasku et al., Kew Bull. 70: 23. 2015.

Guatteria sempervirens Dunal, Monogr. Anonac. 133. 1817. Lecto (designated by Turner in press): Rheede, Hort. Malab. 5: t. 16. 1685.
= ***Huberantha korinti*** (Dunal) Chaowasku in Chaowasku et al., Kew Bull. 70: 23. 2015.

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