

A REVISION OF *GUAREA* (MELIACEAE)

T. D. PENNINGTON¹ & J. J. CLARKSON²

The species of *Guarea* F.Allam. ex L. (Meliaceae) are revised. Sixty-nine species are recognised, a key to the species is provided, all names are typified and descriptions of all species are given. A phylogenetic analysis based on ITS sequence data is discussed. Six new species and one new subspecies are described. Five new combinations for subspecies are made.

Keywords. *Guarea*, Meliaceae, neotropics, phylogeny, taxonomic revision.

INTRODUCTION

Guarea F.Allam. ex L. is the second largest genus (after *Trichilia* P.Browne) of American Meliaceae, with 69 species included in the present account. It is placed in the subfamily Melioideae (Pennington & Styles, 1975; Muellner *et al.*, 2003), where it is most closely related to two other small genera, *Ruagea* Karst. and *Heckeldora* Pierre (Muellner *et al.*, 2006, 2008). *Guarea* is separated from all other genera by the combination of the pinnate leaves nearly always with a terminal bud which shows periods of growth between periods of dormancy, the flowers with 4 petals, stamens completely fused into a staminal tube bearing the anthers in the throat, the ovary supported on a broad stipitate nectary-disk and with a discoid style-head, the fruit a loculicidal capsule with fleshy seeds surrounded by a sarcotesta and the embryo with superposed cotyledons.

The related *Ruagea* and *Heckeldora* are easily separable. *Ruagea* differs in its leaves which lack the dormant apical bud, in having 5 imbricate sepals (mostly 4 sepals and always with open aestivation in *Guarea*), 5 petals (mostly 4 or 6 in *Guarea*), 3-locular ovary (mostly 4- or 6-locular in *Guarea*), seed with a swollen basal sarcotesta (absent in *Guarea*) and embryo with collateral cotyledons (nearly always superposed in *Guarea*).

Heckeldora differs in its leaves which lack the dormant apical bud, in having imbricate petals (nearly always valvate in *Guarea*), in its unilocular ovary with parietal placentas (mostly 4–6-locular with axile placentation in *Guarea*), and in the fruit which is a fleshy berry (always a loculicidal capsule in *Guarea*).

¹ Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK. E-mail: t.pennington@kew.org

² Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK. E-mail: j.clarkson@kew.org

The American species of *Guarea* are distributed from northwestern Mexico to northern Argentina. The majority of species occur in Amazonia but a substantial number extend into Central America, the West Indies and coastal Brazil. Virtually all species of *Guarea* are inhabitants of lowland rain forest below 1000 m altitude. A few Andean species, such as *Guarea kunthiana*, reach 2500 m altitude in wet montane forest and in the West Indies a few, such as *G. jamaicensis* and *G. sphenophylla*, are found in seasonally dry forest over limestone. All *Guarea* species are evergreen trees or treelets, even where they occur in a strongly seasonal climate as on the Pacific coast of Central America. Under these conditions they are confined to shady canyons, riversides and other situations with a plentiful supply of ground water.

The genus was last revised in *Flora Neotropica* (Pennington *et al.*, 1981) and since that date a considerable number of new species have been published in local and regional accounts (Pennington & Görts van Rijn, 1984; Pennington, 1986; Pennington & Mori, 1993; Palacios, 1994; Pennington & Edwards, 2001; Pennington & Styles, 2001; Coronado, 2006; Pennington, 2006; Rodríguez, 2006; Palacios, 2007, Pennington & Biggs, in press). In addition to the discovery of new species the boundaries of the genus itself have been refined. Recent molecular phylogenetic studies have shown that *Guarea* is now an exclusively American genus (Koenen & de Wilde, 2012; Koenen *et al.*, in prep.), and the African species are now considered to belong in two separate genera.

There are now 69 species in the genus compared with 37 in 1981. This includes 32 new species and a further six species due to the reassessment of the *Guarea glabra* complex. A total of 3500 new (post-1981) collections have been examined during this study, necessitating the revision of all the distribution maps. The new distribution maps presented here, which show the pre- and post-1981 ranges, demonstrate the imperfect state of knowledge of the genus in 1981. The maps are to be found on pp. 332–345.

In the *Flora Neotropica* treatment (Pennington *et al.*, 1981), it was not possible to formally subdivide the genus on the basis of the morphological variation. However, the species were keyed out into two major groups based on flower size and the number of ovules in the ovary loculi. The significance of these groups has been tested here in a preliminary phylogeny based on sequence data from the ITS locus of ribosomal DNA, which shows that these characters are of little evolutionary significance.

PHYLOGENETIC ANALYSIS

J. J. Clarkson, T. D. Pennington, G. Haynes, R. Engstrand, M. Kaye & M. W. Chase

When it was last revised (Pennington *et al.*, 1981), the largely American genus *Guarea* contained a few African species. However, as a result of recent molecular phylogenetic studies (Koenen & de Wilde, 2012; Koenen *et al.*, in prep.), the African species are now regarded as two separate genera, leaving *Guarea* as exclusively American. On morphological grounds American *Guarea* was assumed to be a monophyletic group, based on a unique combination of several characters, namely the

pinnate leaves with a terminal bud with intermittent growth, flowers with a complete staminal tube bearing stamens within the throat, the ovary supported on a broad nectar-secreting stipe and the loculicidal capsule containing fleshy seeds with a fleshy sarcotesta. In order to test this proposed monophyly three related genera were used as outgroups.

- 1 *Ruagea* (Andean South America). This is morphologically the most similar American genus. It has always been associated with *Guarea*, and at one time was included within it (de Candolle, 1878).
- 2 *Heckeldora* (West Africa). Also morphologically similar to *Guarea* and formerly included within it (Harms, 1940).
- 3 *Turraeanthus* (West Africa). Differs from *Guarea* only in the fusion of the petals and a few other minor characters and always regarded as a close relative of *Guarea*.

All three outgroups were included in the tribe Guareeae in a comprehensive generic review (Pennington & Styles, 1975) and in a broadly based molecular phylogenetic study (Muellner *et al.*, 2008). Forty-seven accessions representing 43 species, out of a total of 69 known species, were included in this study. These cover most of the range of variation and all of the geographical range of the genus. For a list of herbarium specimens sampled see Appendix 1.

MATERIALS AND METHODS

For extractions, a maximum of 0.2 g of dried material was used. DNA was extracted using a modified Doyle & Doyle (1987) 2X CTAB method. DNA was precipitated in isopropanol (-20°C) for two weeks and then re-suspended in 1.55 g/ml caesium chloride/ethidium bromide. Samples were then purified using a density gradient, followed by removal of the ethidium bromide with butanol and caesium chloride by dialysis; all DNAs were stored in 10 mM TE (pH 8).

The ITS region sequenced for this investigation is the standard ribosomal locus used in plant molecular phylogenetics. It therefore includes a small portion of the 3-prime end of the 18S gene, the internal transcribed spacer (ITS) 1, the entire 5.8S gene, the ITS2 and a small portion of the 5-prime end of the 26S gene. Many DNA extracts showed degradation due to the slow drying process associated with the production of herbarium sheets. Therefore, we amplified the ITS region in two halves. Primers ITS5-Mel to ITS2-Mel produced a fragment that was approximately 360 bps. Primers ITS3 to ITS4 produced a fragment that was approximately 390 bps. The overlap between these fragments was small (approximately 15 bps) so they were analysed as interleaved data blocks and not forced into contigs.

Target regions were amplified in a Gene AmpTM 9700 PCR system (ABI, Applied Biosystems, Inc., Warrington, Cheshire, UK) using ReddyMix PCR Mastermix at 2.5 mM MgCl₂ concentration (AB gene, Epsom, Surrey, UK). DMSO was added (4% of total reaction volume) in order to eliminate the secondary structure associated with

TABLE 1. Primers used in this study

Name	Sequence	Reference
ITS2-Mel	GCT ACG TTC TTC ATC GAT GC	Muellner <i>et al.</i> (2005)
ITS5-Mel	GGA AGG AGA AGT CGT AAC AAG G	Muellner <i>et al.</i> (2005)
ITS3	GCA TCG ATG AAG AAC GCA GC	Baldwin (1992)
ITS4	TCC TCC GCT TAT TGA TAT GC	Baldwin (1992)

ribosomal DNA. Table 1 gives details of the primers used. The region was amplified using the following program: 2 minutes at 94°C followed by 30 cycles of 1 minute at 94°C, 1 minute at 50°C, and 1.5 minutes at 72°C (followed by a final extension of 6 minutes at 72°C). All taxa could be sequenced directly from the PCR products and so no bacterial cloning was required.

Prior to cycle sequencing, PCR products were cleaned using NucleoSpin® Extract II mini-columns (Macherey-Nagel, Duren, Germany) following the manufacturer's protocols. Precipitation in ethanol (using both sodium acetate and EDTA) was used to clean cycle sequencing products. Cleaned samples were analysed on an Applied Biosystems Inc. (ABI) 3730 capillary DNA sequencer using Big Dye terminator v3.1 chemistry, following the manufacturer's protocols (ABI).

The raw sequences were edited and assembled using Sequencher version 4.1 (Gene Codes, Inc., Ann Arbor, Michigan, USA). The initial alignment was provided by Clustal X2.0 (The Conway Institute, University College Dublin, Ireland) before being further refined by eye. Gaps were coded as missing data (rather than an additional character state) and thus excluded from the analysis.

Parsimony analysis methods

PAUP version 4.0b (Swofford, 2001) was used for parsimony analysis. For full searches, 50 terminals were included. Heuristic searches were performed using tree bisection-reconnection (TBR) branch swapping and 1000 replicates of random taxon addition were performed with 10 trees held at each step to reduce time searching for suboptimal trees (Salamin *et al.*, 2003). All character transformations were treated as equally likely and unordered (Fitch, 1971). DELTRAN character optimisation was used to illustrate branch lengths throughout (due to reported errors with ACCTRAN optimisation in PAUP v.4.0b). To assess internal support, 1000 bootstrap replicates (Felsenstein, 1985) were performed with equal weights using TBR branch swapping with 10 trees held at each step and simple taxon addition.

Bayesian analysis methods

Bayesian analysis was performed using MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001). An HKY85 model was specified in which all transitions and

transversions have potentially different rates. More complex models were also used, but these provided the same tree with similar posterior probabilities (PP; results not shown). Analyses were performed with 500,000 generations of Monte Carlo Markov chains with equal rates and a sampling frequency of 10. Three separate runs were performed to ensure that the analysis was producing consistent results. Microsoft Excel was used to plot generation number against lnL to find the 'burn in'. Trees of low PP were deleted, and all remaining trees were imported into PAUP v.4.0b. A majority rule consensus tree was produced showing the frequencies (i.e. posterior probabilities) of all observed bi-partitions.

Parsimony analysis results

The total number of characters was 697, of which 312 were variable (44.76%) and 182 (26.11%) were potentially parsimony informative. Analysis produced 2171 equally most-parsimonious trees (length = 702 steps; consistency index, CI (including autapomorphies) = 0.64; retention index, RI = 0.79). One of the most-parsimonious trees with its Fitch branch lengths (DELTRAN optimisation) is shown in Fig. 1. This tree is presented in two parts (A and B) but is the result of a single analysis. Clades not found in all shortest trees are marked with arrowheads. Bootstrap percentages (BP) equal to or greater than 50 that are consistent with the strict consensus tree are shown below each branch.

Bayesian analysis results

The 'burn-in', 2500 trees of low likelihood, were omitted from the consensus tree. Bayesian analysis produced the same overall topology as did parsimony (Fig. 1 versus Fig. 2). All of the clades that differ have low BP in parsimony analysis and low PP in the Bayesian tree, although the general trend is that the Bayesian posterior probabilities are higher than bootstrap percentages.

As mentioned the trees only differ for clades which are weakly supported (both BP and PP). A typical example is the sister group of the well-supported (BP 98, PP 1.0) small Central American clade consisting of *Guarea macrocalyx*, *G. tafae-malekui* and *G. zarceroensis*. In both analyses the Central American clade has three South American successive sister species (*Guarea pubescens*, *G. subandina* and *G. michel-moddei*). However, the branching order of these successive sisters is different in the two analyses. Each has no bootstrap support in the parsimony analysis (Fig. 1) and only weak PPs (0.22, 0.37) in the Bayesian analysis (Fig. 2) and so this is not a hard incongruence.

MONOPHYLY AND INFRA-GENERIC CLASSIFICATION

The analysis confirms the monophyly of American *Guarea*, and demonstrates that two ancestral South American species, *G. silvatica* and *G. anomala*, form early diverging isolated lineages with long branch lengths (Fig. 1A). In contrast the

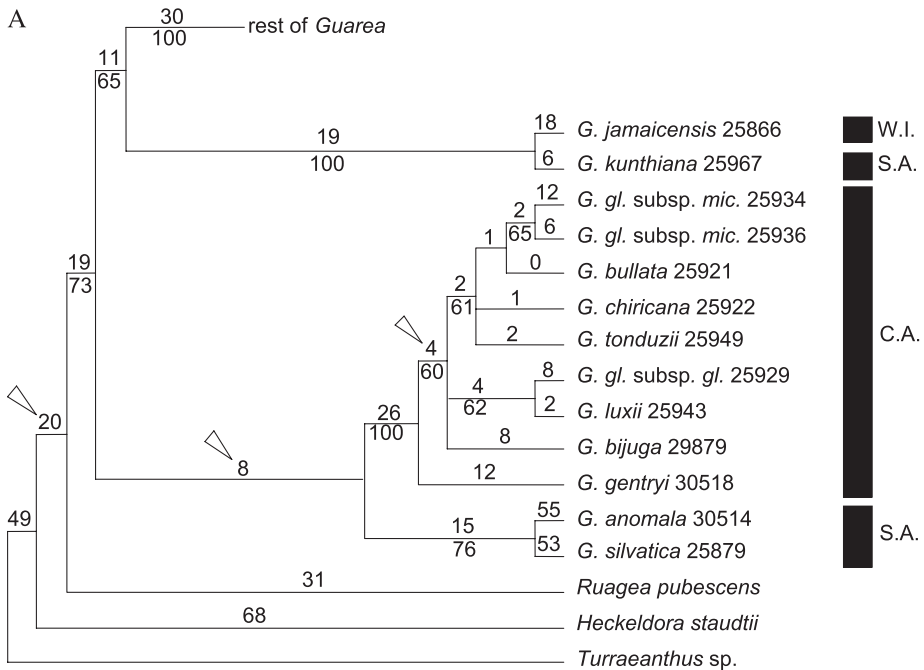


FIG. 1A. Part of one of the most-parsimonious trees for *Guarea* obtained from analysis of ITS sequences. Bootstrap values, above 50%, are shown below branches and branch lengths are shown above branches. Arrows indicate groups not present in all shortest trees. The black bars indicate distribution data with S.A. representing South America, C.A. representing Central America and W.I. representing the West Indies. Species with subspecies are represented by the following abbreviations: *G. gl. subsp. gl.* represents *G. glabra* subsp. *glabra* and *G. gl. subsp. mic.* represents *G. glabra* subsp. *microcarpa*. Kew DNA bank numbers are shown after each taxon name.

majority of the remaining species are located in two major clades, one South American and the other Central American, whose constituent species are on very short branch lengths. The major division of the genus therefore falls along geographical and not morphological lines. In the most recent monograph of the genus (Pennington *et al.*, 1981), no formal morphological infra-generic classification was proposed. This was because of an absence of unique characters which could be used to define species groups. All species were defined on the basis of unique combinations of often quantitative characters, without distinct character states. However, in the key to the species there was an informal division of the genus based on the size of the flower, the number of ovary locules and number of ovules (flowers < 10 mm long, ovary 4-locular and locules 1-ovulate versus flower > 10 mm long, ovary 4–10-locular and locules 2-ovulate). If these characters are placed onto a phylogenetic tree (Fig. 1B or Fig. 2), they do not support any monophyletic groups, as both character states are distributed throughout the large South American clade, so any formal arrangement based on them would have no evolutionary basis.

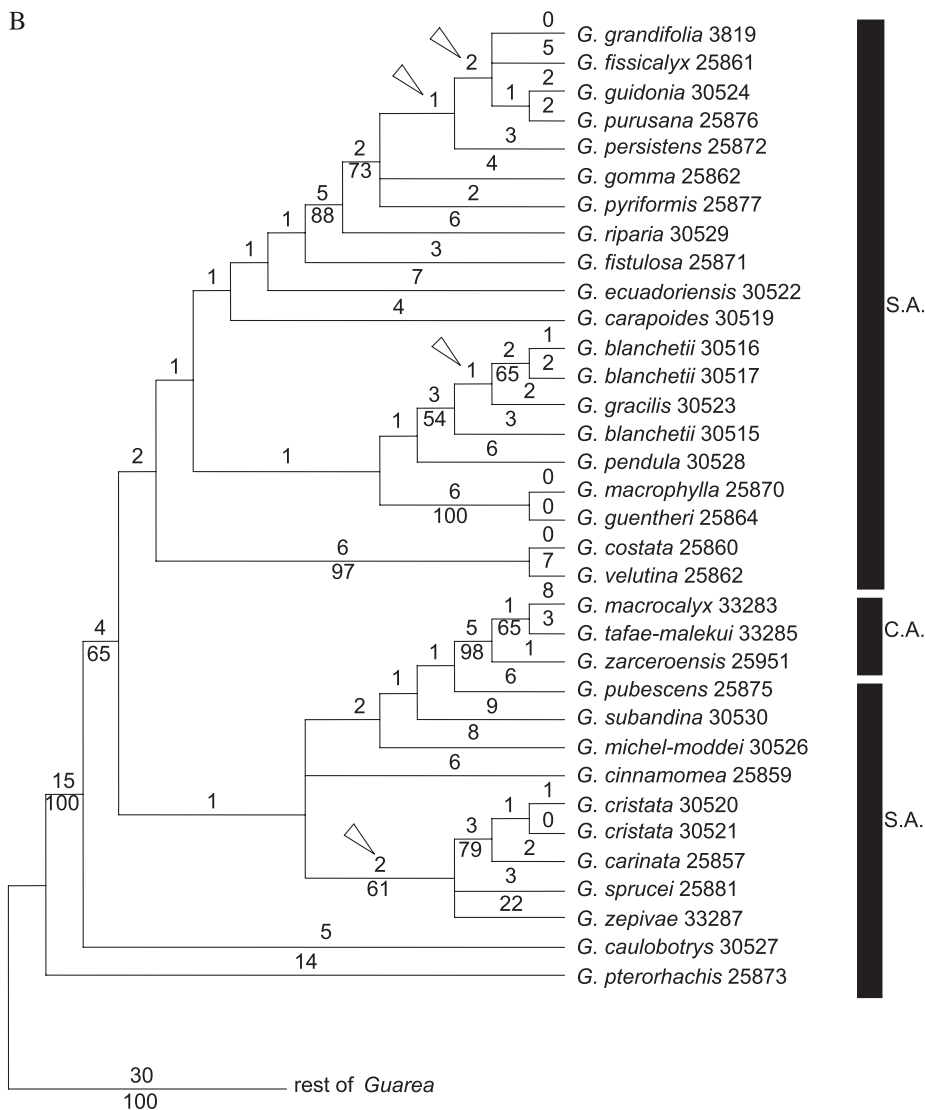


FIG. 1B. Part of one of the most-parsimonious trees for *Guarea* obtained from analysis of ITS sequences. Bootstrap values, above 50%, are shown below branches and branch lengths are shown above branches. Arrows indicate groups not present in all shortest trees. The black bars indicate distribution data with S.A. representing South America and C.A. representing Central America. Kew DNA bank numbers are shown after each taxon name.

It should be noted that the genus *Guarea* is monophyletic as demonstrated by most previous studies (e.g. Muellner *et al.*, 2006, 2008). This can be contrasted with the study of Fukuda *et al.* (2003) in which *Guarea* was not monophyletic although this unusual result was probably due to insufficient taxon sampling and also a lack of informative characters.

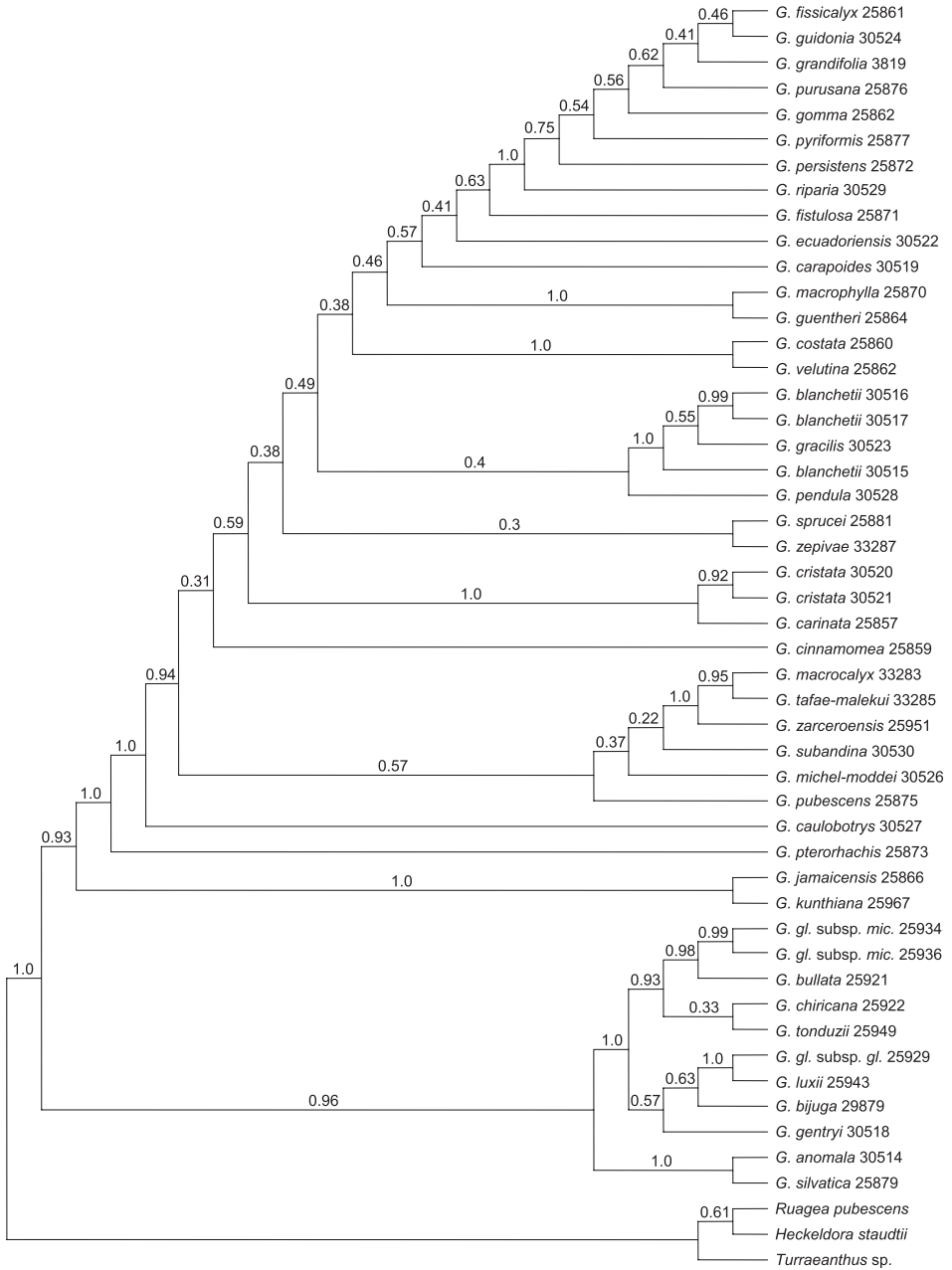


FIG. 2. Bayesian analysis of *Guarea* using ITS sequences. Tree shown is a consensus of 47,500 trees with posterior probabilities shown above branches.

SPECIES DELIMITATION

Where several individuals of the same species were sampled, they were found to have very similar ITS sequences (e.g. *Guarea cristata*, *G. glabra* subsp. *microcarpa*), lending support to the morphological species delimitation used in this monograph. Three accessions of *Guarea blanchetii* were sampled and a high amount of intra-species variation was detected (each of the accessions in Fig. 1B has autapomorphies). These data also show that the species might not be monophyletic due to placement of *Guarea gracilis*. However, the embedding of *Guarea gracilis* within *G. blanchetii* is not present in all shortest trees (Fig. 1B) so this question is unresolved. Additionally this relationship receives only weak support (PP 0.55) in the Bayesian analysis (Fig. 2).

There are a few obviously morphologically distinct species within the genus, and it is significant that the ITS phylogeny confirms their isolated position, as they all occur at the end of long branches. They are *Guarea silvatica*, *G. anomala*, *G. jamaicensis*, *G. kunthiana* and *G. pterorhachis*. In contrast, the remaining species in both the South American and Central American clades are separated by short branch lengths, suggesting a more recent rapid radiation.

The most useful morphological differences between *Guarea* species are in the fine structure of the fruit (e.g. ornamentation of the pericarp) and in the fruit size. This contrasts with the general uniformity in vegetative and floral characters. It is clear from the present analysis, however, that species with large differences in the size and ornamentation of the fruit are often separated by very short genetic distance. For example, *Guarea riparia* (small, smooth fruit), *G. fistulosa* (medium-sized, strongly ribbed fruit) and *G. ecuadoriensis* (large smooth fruit) are genetically close. Just as gross fruit characters are of little value in determining family relationships (e.g. Meliaceae containing capsules, berries and drupaceous fruits), so at the species level it appears that fine fruit structure is of little value in determining relationships.

The low sequence divergence between species in the South American and Central American clades may account for the difficulty in morphological species delimitation due to insufficient time for morphological divergence. Similar patterns of recent rapid radiation have been postulated for other genera of tropical American trees, for example *Guatteria* Ruiz & Pav.: Annonaceae (Erkens *et al.*, 2007), *Inga* Mill: Leguminosae (Richardson *et al.*, 2001), *Aglaiia* Lour. (compare Muellner *et al.*, 2005, 2008) and *Trichilia* P.Browne: Meliaceae (Pennington *et al.*, in prep.).

The South American clade (*Guarea grandifolia* to *G. pterorhachis*) is predominantly Amazonian, the only exceptions being a small group of coastal Brazilian species (*G. blanchetii*, *G. gracilis* and *G. pendula*), a small group of species confined to Costa Rica (*G. zarceriensis*, *G. macrocalyx* and *G. tafae-malekui*) and *G. caulobotrys* and *G. pyriformis* (coastal Pacific Colombia, Panama and Costa Rica). Several of the widespread Amazonian species now extend into Panama and Costa Rica (e.g. *Guarea pterorhachis*, *G. macrophylla*, *G. guidonia*, *G. grandifolia*).

The Central American clade (*Guarea glabra* to *G. gentryi*) consists entirely of *G. glabra* and its close relatives. Most of these species were previously included in

a broadly defined and widely distributed *Guarea glabra* (Pennington *et al.*, 1981) within which they were treated as informal ‘races’. Recent multivariate analysis of the Central American component of the group (Coronado, 2003) showed that these races were morphologically discrete, at least in morphospace, and should be recognised as distinct species, a course which has been followed in some cases in this revision. The ITS phylogeny sheds an interesting light on the relationships of the species within this complex. It shows that different accessions of *Guarea glabra* are paraphyletic with respect to *G. luxii* and *G. bijuga*. This suggests that these two splits from what was formerly regarded as a single variable species may have arisen from the wider *Guarea glabra*.

The ITS phylogeny shows that the components of the *Guarea glabra* complex comprise a group of closely related taxa with little genetic distance between them. For example, only four substitutions separate *Guarea bullata*, *G. chiricana* and *G. tonduzii*, far less than the distance separating two accessions of *G. glabra* subsp. *microcarpa*. The problem remains of whether to recognise these taxa as distinct species, or as a single species divided into several subspecies, or a single species with informal races. In view of the poor morphological distinction between some of the component taxa (many intermediate specimens), a middle course has been taken, with the most morphologically distinct taxa being recognised at the species level, while the less distinct are retained as subspecies within the wider *Guarea glabra*. The decision is a practical one which does not necessarily strictly follow the ITS phylogeny results. Unfortunately it was not possible to include samples of this complex from the West Indies and northern South America which are required to complete this picture. This preliminary analysis highlights the importance of sampling throughout the range of a complex like *Guarea glabra* and its relatives before making taxonomic decisions.

The present-day *Guarea* flora of Central America therefore comprises three elements:

- 1 The *Guarea glabra* complex (*G. glabra*, *G. bullata*, *G. chiricana*, *G. tonduzii*, *G. luxii*, *G. bijuga*, *G. gentryi*) which, together with *G. anomala* and *G. silvatica*, form a sister group to the whole of the rest of *Guarea* with a relatively ancient origin.
- 2 Those species which have arisen more recently from the South American stock, which are now confined to Costa Rica (*Guarea macrocalyx*, *G. tafae-malekui*, *G. zarceroensis*).
- 3 South American species with slight range extensions into Panama or Costa Rica, such as *Guarea guidonia*, *G. pterorhachis* and *G. macrophylla*.

THE DIVERGENCE OF SPECIES

In our analyses *Guarea silvatica* and *G. anomala* are on long branches (with 53 and 55 substitutions respectively in the parsimony tree; Fig. 1A). The two species appear to have diverged long ago from all other species sampled (as judged by branch

lengths). They are also distinctive species morphologically and each has a unique character or combination of characters. *Guarea silvatica* lacks the terminal leaf bud (present in nearly all species of the genus), has imbricate petals (usually valvate), a bony seed coat (usually fleshy) and an embryo with collateral cotyledons (nearly always superposed).

Guarea anomala has alternate leaflets (usually opposite) and lacks the terminal leaf bud, has unusual venation, and flowers with 3 petals (usually 4–6). Other morphological data, such as the complete staminal tube with the anthers inserted within the throat, the ovary structure, and the DNA sequence data, unequivocally support both species belonging in *Guarea* (BP 73, PP 1.0) but their uniqueness in the genus is noteworthy. We were able to add another representative of *Guarea silvatica* from a published project on DNA barcoding (Gonzalez *et al.*, 2009) to test the position of our sample. Analyses showed that this published sequence was nearly identical, and sister, to our sample (data not shown). The few substitutions that differed are not surprising due to the great geographical distance between the two collection localities (our sample was collected in Brazil (Manaus) and Gonzalez *et al.* (2009) collected in French Guiana).

The large Central American clade consists of nine taxa on a relatively long branch (26 substitutions in Fig. 1A) but there is much less variation between taxa (e.g. only four substitutions separate *Guarea bullata*, *G. chiricana* and *G. tonduzii*). This suggests the long distance dispersal of an ancestral species to Central America followed by a recent radiation of the extant taxa.

Guarea pterorhachis, *G. jamaicensis* and *G. kunthiana* are all on long branches and are successive sisters to the South American clade. They are the earliest diverging lineages within the clade and therefore may have some ancestral characteristics of the group. *Guarea pterorhachis* is separated by 29 substitutions (14 + 15) from the ‘core’ South American clade (Fig. 1). It differs from all other species of the genus in its broadly winged leaf rhachis and other rarely encountered floral characters. *Guarea jamaicensis* is separated by 67 substitutions (18 + 19 + 30) from the *Guarea pterorhachis* branch. *Guarea jamaicensis* is found only in Jamaica, along with *G. glabra*, and since these two species are not related they must represent two separate colonisation events. It is easily recognised by the small rounded leaflets. *Guarea kunthiana* has 55 substitutions (6 + 19 + 30) from the *G. pterorhachis* branch. This species has a very characteristic leaf venation and colour which enable it to be readily identified in the vegetative state, although its floral and fruit structure is typical of the genus. The remaining species within the South American clade are on very short branches suggesting recent speciation. This is by far the largest clade in the genus with 35 species sampled in this phylogenetic analysis. Within the South American clade there is a small and well-supported Central American clade (BP 98, PP 1.0) which consists of *Guarea macrocalyx*, *G. tafae-malekui* and *G. zarcerensis*. This small Central American group appears to be recently descended from the South American group (according to the short branch lengths) and its ancestors must have dispersed to Central America and then speciated into the three extant species.

NOTES ON THE SYSTEMATIC TREATMENT, ABBREVIATIONS, ETC.

Species arrangement for species 1–42 follows the order indicated by the ITS phylogeny (Fig. 1A & 1B). The remaining species are in alphabetical order (no ITS sequence data available).

Descriptions and measurements of vegetative characters are from dried specimens. Twig diameter is measured 10–20 cm below the shoot apex on a fertile shoot. Leaf measurements are from fertile specimens, unless otherwise stated. Descriptions and measurements of floral characters are from rehydrated specimens or specimens preserved in spirit.

Full species descriptions are given only to new species, species described since 1981, or species imperfectly known in 1981. All other species are given an abbreviated description.

Specimen citation in the text

Collections examined means that all specimens (pre and post 1980) seen are cited except for type specimens which are listed after the publication details. *Representative additional collections* means that only one specimen (post 1980) from each major political division of a country is cited. *Additional collections examined* means all specimens (post 1980) are cited. All specimens seen in this study are cited in the List of Exsiccatae.

Geographical coordinates are given as 1 degree squares, e.g. NW1067 means 10°N, 67°W.

The List of Exsiccatae contains mainly collections made after 1980, plus a few earlier ones mentioned in the text, such as types.

SYSTEMATIC TREATMENT

Guarea ('Guara') F.Allam. in L., Mant. 150, 228 (1771), nom. cons.; C.DC. in Mart., Fl. Bras. 11(1): 181 (1878); C.DC. in A.DC. & C.DC., Monogr. Phan. 1: 542 (1878); Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19b1: 129, t. 31, figs R–X (1940), p.p.; T.D.Penn. & Styles, Blumea 22: 494, fig. 12a, b (1975), p.p.; T.D.Penn. in T.D.Penn. et al., Flora Neotrop. 28: 255 (1981); T.D.Penn. & Görts, Fl. Suriname 5(1): 519 (1984); T.D.Penn., Bol. Técn. Centro Pesq. Cacao 143: 1 (1986); W.Palacios, Novon 4: 155 (1994); M.E.Morales, Revista Acad. Colomb. Ci. Exact. 22(82): 335 (1998); T.D.Penn. & K.S.Edwards, Fl. Venez. Guayana 6: 528 (2001); T.D.Penn. & Styles, Fl. Nicaragua 2 (Meliaceae): 1419 (2001); Coronado, Novon 16: 462 (2006); T.D.Penn., Rodriguesia 57(2): 209 (2006); Al.Rodr., Lankesteriana 6: 101 (2006); W.Palacios, Fl. Ecuador 82, Fam. 98, Meliaceae: 1 (2007). – Type species: *Guarea trichilioides* L. (= *Guarea guidonia* (L.) Sleumer). For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 255 (1981).

Trees or treelets. *Bud scales* absent. *Indumentum* of simple hairs. *Leaves* nearly always paripinnate with a terminal bud usually showing intermittent growth, rarely without a terminal bud, rarely alternate. *Leaflets* sometimes glandular-punctate or -striate. *Inflorescence* axillary or clustered immediately below the leaves, or ramiflorous on larger branches or cauliflorous, a panicle, often with cymose branches (thyse), raceme or spike. *Flowers* unisexual, plant dioecious. *Calyx* with an almost entire margin or shallowly to deeply 3–7-lobed, aestivation open. *Petals* (3–)4–6(–7), free, nearly always valvate, rarely slightly imbricate. *Stamens* completely united into a cylindrical staminal tube, sometimes contracted at the throat, margin entire, crenate or with short truncate or emarginate lobes; anthers (7–)8–12(–14), glabrous, inserted within the throat of the staminal tube, completely included or partly exerted, alternating with the lobes, antherodes similar, smaller, without pollen. *Nectary* short-to long-stipitate, nearly always expanded to form a collar below the ovary. *Ovary* 2–10(–14)-locular, locules with 1–2(–4) superposed ovules, style-head discoid, pistillode smaller, less swollen, with well-developed non-functional ovules. *Fruit* a 2–10(–14)-valved loculicidal capsule, locules 1–2(–4)-seeded; pericarp leathery or woody, endocarp thin, cartilaginous. *Seed* often shaped like the segment of an orange, with a thin fleshy sometimes vascularised sarcotesta. *Embryo* with thick plano-convex, superposed or rarely collateral cotyledons; radicle abaxial, extending to the surface; when cotyledons collateral then radicle apical. *Endosperm* absent.

Distribution. Sixty-nine described species in tropical America.

Key to the species of Guarea

- 1a. Petals generally 4–10 mm long, ovary (2–)4–6(–9)-locular, locules 1-ovulate, capsule (3–)4–6(–9)-valved, valves 1-seeded _____ 2
- 1b. Petals generally 10–20 mm long, ovary 2–12-locular, locules with 2(–4) superposed ovules, capsule 4–12-valved, valves with 1–2(–4) superposed seeds _____ 45
- 2a. Capsule at least 3.5 cm long _____ 3
- 2b. Capsule usually 1–2.5 cm long, never more than 3.5 cm long _____ 7
- 3a. Leaves without a terminal bud, ovary 2–3(–4)-locular, glabrous, capsule constricted between the seeds _____ **1. *G. silvatica***
- 3b. Leaves with a terminal bud, ovary (3–)4–6(–7)-locular, pubescent or strigose, capsule not constricted between the seeds _____ 4
- 4a. Capsule 7–8 cm long, prominently longitudinally ribbed (ribs 3–4 mm high) _____ **59. *G. megacostata***
- 4b. Capsule 3.5–6.2 cm long, smooth or only faintly lined _____ 5
- 5a. Secondary veins 7–11 pairs, petals 6–7.5 mm long _____ **47. *G. convergens***
- 5b. Secondary veins 12–18 pairs, petals 8–14 mm long _____ 6

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- 6a. Petals 8–12 mm long, inflorescence 15–40 cm long, capsule \leq 4 cm long _____ **37. *G. gomma***
- 6b. Petals 11.5–14 mm long, inflorescence 3–15 cm long, capsule 5–6.2 cm long _____ **18. *G. cinnamomea***
- 7a. Tufts of hair present in the axils of the secondary veins on leaflet lower surface _____ 8
- 7b. Axillary hair tufts absent _____ 9
- 8a. Leaflets usually glabrous (apart from hair tufts in vein axils), petals 4–9 mm long, inflorescence a simple panicle, with a few lateral branches _____ **6. *G. glabra***
- 8b. Lower leaflet surface sparsely and minutely appressed puberulous with pale whitish hairs, petals 3–4 mm long, inflorescence a profusely branched panicle, usually with several branches from the base _____ **3. *G. gentryi***
- 9a. Leaves without a terminal bud, leaflets alternate, petals 3–4 _____ **2. *G. anomala***
- 9b. Leaves with a terminal bud, leaflets opposite, petals 4–6 _____ 10
- 10a. Petiole 1–2 mm long, basal pair of leaflets greatly reduced, $1-4.2 \times 1-3.2$ cm, broadly ovate to suborbicular _____ **66. *G. subsessilifolia***
- 10b. Petiole at least 2 cm long, basal pair of leaflets not greatly reduced, not broadly ovate or suborbicular _____ 11
- 11a. Leaflets $6-14.2 \times 0.9-2.8$ cm, 5–6 times as long as broad, narrowly elliptic, species confined to rocky riversides _____ **35. *G. riparia***
- 11b. Leaflets broader (less than 5–6 times as long as broad), species not confined to rocky riversides _____ 12
- 12a. Twigs hollow, calyx persistent in young fruit, pedicel 5–6(–10) mm long _____ **38. *G. persistens***
- 12b. Twigs not hollow, calyx not persistent, pedicel shorter _____ 13
- 13a. Fruit smooth _____ 14
- 13b. Fruit ribbed, winged or tuberculate _____ 34
- 14a. Mature fruit tomentose, pubescent or puberulous _____ 15
- 14b. Mature fruit glabrous _____ 25
- 15a. Lower lamina with dense crisped matted puberulous hairs, petals c.12.5 mm long, fruit densely puberulous _____ **50. *G. crispa***
- 15b. Indumentum of lower lamina not of dense crisp matted puberulous hairs, petals not more than 12 mm long, usually much less, fruit puberulous or not _____ 16
- 16a. Petiole and rhachis soon becoming woody, leaflets 6.5–8.5 cm long, broadly elliptic to obovate, apex obtuse or rounded, c.2 times as long as broad, coriaceous, inflorescence 2–6-flowered, 2–3 cm long _____ **11. *G. jamaicensis***

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- 16b. Petiole and rhachis not woody (except when old), leaflets usually longer, if as small then at least 3 times as long as broad, not coriaceous and with a much longer many-flowered inflorescence _____ 17
- 17a. Lower lamina pubescent or puberulous _____ 18
- 17b. Lower lamina \pm glabrous _____ 21
- 18a. Tertiary veins numerous, fine, parallel, ovary short, rounded at the apex, densely long-strigose, capsule depressed-globose or globose, usually coarsely pubescent _____ **21. *G. pubescens***
- 18b. Tertiary veins not finely parallel and oblique, ovary tapering at the apex, pubescent, capsule pyriform to globose, minutely puberulous or shortly pubescent _____ 19
- 19a. Young shoots, inflorescence and lower lamina with yellowish pubescence, capsule pyriform, 2.3–3 cm long, minutely puberulous, pericarp 2–4 mm thick _____ **36. *G. pyriformis***
- 19b. Indumentum of young shoots, inflorescence and lower lamina not yellowish, capsule globose, or if pyriform then pericarp 1–2 mm thick _____ 20
- 20a. Young shoots golden-tomentose, leaves coriaceous, petals 8–12 mm long, capsule globose, 1.5–2.8 cm diam., sparsely to densely pubescent, pericarp 1.5–3 mm thick _____ **7. *G. tonduzii***
- 20b. Young shoots minutely puberulous to pubescent, leaves not coriaceous, petals mostly 6–9 mm long, capsule globose or pyriform, 0.75–2.5(–3.5) cm long, minutely puberulous to pubescent, pericarp 1–2 mm thick _____ **28. *G. macrophylla***
- 21a. Tertiary veins numerous, fine, parallel, oblique, ovary short, rounded at the apex, densely long-strigose, capsule depressed-globose or globose, usually coarsely pubescent _____ **21. *G. pubescens***
- 21b. Tertiary veins not finely parallel and oblique, often obscure, ovary tapering at the apex, pubescent or strigose, capsule pyriform to globose, minutely puberulous or shortly pubescent _____ 22
- 22a. Leaves with indeterminate apical growth, petals 4–5, anthers nearly always 8 _____ 23
- 22b. Leaves without indeterminate apical growth, petals 4–6, anthers 8–11 _____ 24
- 23a. Inflorescence a widely branched panicle with long, weak, slender axes, subglabrous _____ **64. *G. scabra***
- 23b. Inflorescence little-branched, pubescent or puberulous _____ **28. *G. macrophylla***
- 24a. Leaflets usually oblong, secondary veins 12–18 pairs, petals 8–12 mm long, fruit 2.5–4 cm long _____ **37. *G. gomma***
- 24b. Leaflets usually elliptic, secondary veins mostly 10–12 pairs, petals 7–8 mm long, fruit 1.5–2.2 cm long _____ **41. *G. fissicalyx***

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- 25a. Leaflets mostly (5.6–)8–11.3(–14.5) × (1.5–)2.5–3.6(–4) cm, secondary veins 12–18 pairs _____ **5. *G. luxii*** 26
- 25b. Leaflets larger, secondary veins usually fewer _____ 26
- 26a. Fruit dark brown, shining, usually with numerous pale lenticels _____
_____ **40. *G. guidonia***
- 26b. Fruit red or pink, often rough-skinned, with or without lenticels _____ 27
- 27a. Whole plant glabrous, leaflets usually 6.7–12 cm broad _____ **4. *G. bijuga***
- 27b. Young shoots and lower leaflet surface pubescent (at least when young), leaflets usually 3–8 cm broad _____ 28
- 28a. Venation impressed on the upper leaflet surface, often strongly so and leaves bullate, petals 7–11 mm long, stiffly appressed pubescent outside _____ **9. *G. bullata***
- 28b. Venation not impressed above or if impressed then petals subglabrous, leaflets not bullate, petals usually smaller _____ 29
- 29a. Young shoots, sepals and outer surface of petals densely pilose-setose _____ **51. *G. donnell-smithii***
- 29b. Young shoots, sepals and petals not pilose-setose _____ 30
- 30a. Leaflets glabrous below _____ **8. *G. chiricana***
- 30b. Leaflets pubescent below _____ 31
- 31a. Finely reticulate higher order venation visible on both surfaces of the leaflet, petals usually glabrous _____ **8. *G. chiricana***
- 31b. Reticulate higher order venation not conspicuous, petals pubescent or puberulous _____ 32
- 32a. Petiole 10–13.5 cm long, leaves with a dormant inactive terminal bud, Mato Grosso, Brazil _____ **14. *G. zepivae***
- 32b. Petiole 2–6 cm long, leaves with a terminal bud showing intermittent growth, Mexico to Honduras _____ 33
- 33a. Calyx shallowly lobed or margin truncate, petals 4–6.5 mm long _____
_____ **6. *G. glabra***
- 33b. Calyx lobed for 1/3 to 1/2 its length, petals c.8 mm long _____ **60. *G. mexicana***
- 34a. Fruit with 12–16 thin convoluted and anastomosing longitudinal wings 5–10 mm deep _____ 35
- 34b. Fruit verrucose, ribbed or shallowly winged, the ribs sometimes torulose or tuberculate _____ 36
- 35a. Young branches velutinous or tomentose, leaflets coriaceous, base obtuse or truncate, tertiary veins obscure, petals 7–10 mm long _____ **25. *G. velutina***
- 35b. Young branches appressed puberulous, leaflets chartaceous, base narrowly attenuate, tertiary venation easily visible, petals c.5.5 mm long _____
_____ **57. *G. juglandiformis***

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- 36a. Leaflets 5–6.5 cm long, c.2 times as long as broad, broadly oblanceolate, obovate or cuneiform, coriaceous, fruit c.1.5 cm diam., tuberculate-ribbed _____ **65. *G. sphenophylla***
- 36b. Leaflets larger, not obovate or cuneiform, if oblanceolate then at least 3 times as long as broad and chartaceous, fruit larger (except *G. gracilis*) _____ 37
- 37a. Secondary veins 23–24 pairs, anthers with a short terminal appendage, ovary 6-locular _____ **58. *G. lozanii***
- 37b. Secondary veins not more than 16 pairs, anthers without a terminal appendage, ovary 4–5-locular _____ 38
- 38a. Fruit contracted at the base into a stipe 0.5–0.8 cm long _____ 39
- 38b. Fruit without a stipe, or if present then only 1–2 mm long _____ 40
- 39a. Leaves without intermittent apical growth, secondary veins 11–16 pairs, ± straight and parallel, petals 9–13 mm long, valves of fruit with 3–5 shallow wrinkled ribs _____ **55. *G. humaitensis***
- 39b. Leaves with intermittent apical growth, secondary veins 8–11 pairs, arcuate and convergent, petals 5.5–6.5 mm long, valves of fruit with 3 ribs or shallow wings, these sometimes anastomosing _____ **26. *G. costata***
- 40a. Tertiary veins numerous, fine, parallel, oblique, ovary short, rounded at the apex, densely long-strigose, capsule depressed-globose or globose, obscurely ribbed and often minutely tuberculate between the ribs, usually coarsely pubescent _____ **21. *G. pubescens***
- 40b. Tertiary venation not finely parallel and oblique, ovary tapering to the apex, pubescent or strigose, capsule obovoid, pyriform, globose or rarely depressed-globose, mostly puberulous _____ 41
- 41a. Leaflets 23–42 cm long, inflorescence cauliflorous or ramiflorous on larger branches _____ **30. *G. blanchetii***
- 41b. Leaflets generally much smaller, inflorescence axillary or in the axils of fallen leaves _____ 42
- 42a. Secondary veins 5–7 pairs, petiolule 1.5–1.7 cm long _____ **22. *G. zarceroensis***
- 42b. Secondary veins 6–14 pairs, petiolule up to 10 mm long _____ 43
- 43a. Fruit obscurely to prominently torulose or verrucose, if ribbed then ribs torulose or verrucose _____ **28. *G. macrophylla***
- 43b. Fruit obscurely to prominently ribbed (ribs not torulose or verrucose) _____ 44
- 44a. Lower leaflet surface uniformly softly pubescent, capsule broadly pyriform, valves shallowly 3-ribbed _____ **29. *G. pendula***
- 44b. Lower leaflet surface with scattered hairs confined to the midrib, capsule depressed-globose, valves prominently 3-ribbed (ribs 2–3 mm high) _____ **31. *G. gracilis***
- 45a. Leaf rhachis broadly winged _____ **12. *G. pterorrhachis***

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- 45b. Leaf rachis unwinged _____ 46
- 46a. Leaflets 32–39 cm long, young shoots and lower leaflet surface hispid with yellow hairs, venation brochidodromous, secondary veins 38–40 pairs _____ **45. *G. casimiriana***
- 46b. Leaflets shorter, or if as long then indumentum not hispid, venation eucamptodromous and secondary veins fewer _____ 47
- 47a. Fruit 9.5–10.5 × 9–9.5 cm, broadly pyriform, pericarp 0.8–1.2 cm thick, valves with 3 longitudinal rounded ribs, ribs branched and tuberculate towards the apex _____ **53. *G. grossa***
- 47b. Fruit smaller, rarely up to 9 cm long, but then without prominent rounded ribs _____ 48
- 48a. Ovary glabrous _____ 49
- 48b. Ovary pubescent _____ 52
- 49a. Leaf without a terminal bud, ovary 2–3(–4)-locular, capsule strongly constricted between the seeds, cotyledons collateral _____ **1. *G. silvatica***
- 49b. Leaf with a terminal bud, ovary (3–)4-locular, capsule not or only slightly constricted between the seeds, cotyledons superposed _____ 50
- 50a. Leaflets with hair tufts in the axils of the secondary veins below _____ **56. *G. inesiana***
- 50b. Leaflets without hair tufts in the vein axils _____ 51
- 51a. Twigs hollow, leaflets 30–50 cm long, petals glabrous _____ **46. *G. constricta***
- 51b. Twigs not hollow, leaflets mostly 15–25 cm long, petals with appressed indumentum outside _____ **10. *G. kunthiana***
- 52a. Leaves strongly bullate _____ 53
- 52b. Leaves not bullate _____ 54
- 53a. Secondary veins 18–23 pairs, inflorescence axillary or on twigs below the leaves, ovary 6–8-locular, fruit 3.5–4 cm long, obovoid _____ **15. *G. sprucei***
- 53b. Secondary veins 23–26 pairs, inflorescence cauliflorous, ovary 4-locular, fruit c.5 cm long, broadly oblong, tapering at the base to a stout stipe c.1 cm long _____ **62. *G. reticulatovenosa***
- 54a. Venation brochidodromous, secondary veins 25–30 pairs _____ **69. *G. venenata***
- 54b. Venation eucamptodromous, or if brochidodromous then secondary veins fewer than 20 pairs _____ 55
- 55a. Leaflets broadly oblanceolate, obovate or cuneiform, 5–8.5 cm long, c.2 times as long as broad, coriaceous, inflorescence 2–3 cm long, 1–6-flowered _____ 56
- 55b. Not with the above combination of characters, leaflets larger or at least 3 times as long as broad, and inflorescence longer and with more flowers _____ 57
- 56a. Fruit smooth _____ **11. *G. jamaicensis***

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- 56b. Fruit tuberculate-ribbed _____ **65. *G. sphenophylla***
- 57a. Indumentum of young parts and lower lamina prominently villose, tomentose, hispid or coarsely pubescent _____ 58
- 57b. Indumentum of young parts finely and minutely puberulous, lower lamina sparsely and minutely puberulous or glabrous _____ 70
- 58a. Fruit winged, ribbed or tuberculate _____ 59
- 58b. Fruit smooth _____ 65
- 59a. Mature capsule with thin fleshy convoluted longitudinal wings _____ 60
- 59b. Mature fruit ribbed or tuberculate _____ 62
- 60a. Ovary 9–10-locular, valves of fruit with a single longitudinal wing _____
_____ **67. *G. talamancana***
- 60b. Ovary 4–8-locular, valves of fruit with several (usually at least 3) longitudinal wings _____ 61
- 61a. Leaves bullate, indumentum of lower leaf surface sparse, confined to midrib and veins, ovary 6–8-locular, fruit 3–4 cm long _____ **19. *G. michel-moddei***
- 61b. Leaves not bullate, lower leaflet surface coarsely and uniformly hirsute, ovary 4–6-locular, fruit 4–6 cm long _____ **17. *G. cristata***
- 62a. Indumentum of lower lamina inconspicuous, shortly and finely pubescent, secondary veins mostly 6–14 pairs, mature fruit ribs tuberculate, ovary usually 4-locular, fruit not exceeding 3.5 cm long _____ **28. *G. macrophylla***
- 62b. Indumentum of lower lamina conspicuous, coarsely pubescent, hirsute or villose, secondary veins more numerous, mature fruit ribbed, not tuberculate, ovary 5- or 6-locular, fruit 3–4.8 cm long _____ 63
- 63a. Inflorescence axillary or on twigs below the leaves, secondary veins (14–)16–20 pairs, petals 14–17 mm long, ovary (4–)5–6(–9)-locular _____ **16. *G. carinata***
- 63b. Inflorescence cauliflorous, secondary veins 18–21 pairs, petals 12–13 mm long, ovary 4-locular _____ 64
- 64a. Leaflets oblanceolate, indumentum of young shoots and lower lamina hirsute-villose _____ **52. *G. eriorhachis***
- 64b. Leaflets broadly oblong to elliptic, indumentum of young shoots and lower lamina puberulous to tomentose _____ **13. *G. caulobotrys***
- 65a. Petals nearly always less than 10 mm long _____ **28. *G. macrophylla***
- 65b. Petals 10–20 mm long _____ 66
- 66a. All parts of shoot, leaves and inflorescence with dense golden tomentose indumentum, leaflets 30–66 cm long, secondary veins 25–33 pairs, petals 18–20 mm long _____ **33. *G. ecuadoriensis***
- 66b. Indumentum mostly pubescent or puberulous, if tomentose, then leaflets much smaller and secondary veins fewer than 20 pairs, petals 10–18 mm long _____ 67

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- 67a. Lower lamina uniformly puberulous with pale whitish crisped hairs _____
 _____ **68. *G. trunciflora***
- 67b. Lower lamina not puberulous with crisped whitish hairs, indumentum generally sparser, pubescent and often confined to midrib and veins _____ 68
- 68a. Secondary veins 16–18 pairs, inflorescence racemose, ovary 4-locular, capsule 4-valved _____ **20. *G. subandina***
- 68b. Secondary veins 11–14 pairs, if more than inflorescence paniculate, ovary (4–)7–10-locular, capsule 5–10-valved _____ 69
- 69a. Twigs slender (3–5 mm diam.), upper lamina with numerous minute raised protuberances, inflorescence usually racemose, rarely a slender panicle, always cauliflorous, petals 15–18 mm long, anthers 2–2.2 mm long _____
 _____ **54. *G. hoffmanniana***
- 69b. Twigs massive (more than 1 cm diam.), upper lamina without raised protuberances, inflorescence a panicle, petals (9–)10–14(–17) mm long, anthers 1.4–1.7(–2) mm long _____ **42. *G. grandifolia***
- 70a. Fruit winged, ribbed or tuberculate _____ 71
- 70b. Fruit smooth or only faintly lined (strongly constricted between the valves in *G. aguilarii*) _____ 78
- 71a. Calyx lobes abruptly contracted into an acumen 1–2 mm long or into a slender subulate point _____ 72
- 71b. Calyx lobes not abruptly contracted into an acumen or subulate point _____ 73
- 72a. Twigs hollow, petals 1.5–1.7 cm long, capsule c.6 × 7 cm, 6–8-valved, slightly tuberculate when dry _____ **23. *G. tafae-malekui***
- 72b. Twigs not hollow, petals 8–14 mm long, capsule c.2 × 2 cm, 4- or 5-valved, valves with 3 shallow longitudinal ribs, ribs tuberculate in the upper half _____
 _____ **24. *G. macrocalyx***
- 73a. Twigs hollow, secondary veins 18–28 pairs, fruit valves 3-winged (wings 2–4 mm deep) _____ **34. *G. fistulosa***
- 73b. Twigs not hollow, secondary veins 12–16, fruit ribbed or tuberculate _____ 74
- 74a. Fruit tuberculate _____ **28. *G. macrophylla***
- 74b. Fruit shallowly ribbed (ribs sometimes tuberculate) _____ 75
- 75a. Dried leaves smell strongly of curry powder, fruit usually botuliform, tapering at the base into a stout stipe c.1 cm long, obscurely ribbed _____
 _____ **27. *G. guentheri***
- 75b. Dried leaves not smelling of curry powder, fruit pyriform to ellipsoid, without a stipe _____ 76
- 76a. Fruit 2–3 cm long _____ **49. *G. corticosa***
- 76b. Fruit 4–8 cm long _____ 77

- 77a. Secondary veins 9–12 pairs, lower lamina puberulous to glabrous, capsule shallowly 12(–15)-ribbed, ribs sometimes torulose _____ **63. *G. rhopalocarpa***
- 77b. Secondary veins 12–16 pairs, lower lamina minutely sericeous at first, becoming glabrous, capsule with c.16 shallow corrugated ribs _____ **48. *G. corrugata***
- 78a. Lower lamina moderately to densely puberulous or pubescent _____ 79
- 78b. Lower lamina glabrous _____ 81
- 79a. Indumentum of young shoots and inflorescence minutely papillose, capsule 3–4 cm long _____ **61. *G. polymera***
- 79b. Indumentum of young shoots and inflorescence puberulous to tomentose, capsule generally smaller _____ 80
- 80a. Indumentum of lower lamina of minute crisped hairs, petals 15–17.5 mm long, ovary 4–6(–7)-locular _____ **44. *G. cartaguenya***
- 80b. Indumentum of lower lamina of straight puberulous hairs, petals (9–)10–14(–17) mm long, ovary (4–)7–8(–10)-locular _____ **42. *G. grandifolia***
- 81a. Ovary locules with (3–)4 superposed ovules, fruit c.6 × 7 cm _____ **23. *G. tafae-malekui***
- 81b. Ovary locules with 1–2 superposed ovules, fruit variable in size _____ 82
- 82a. Fruit less than 2.5 cm long _____ **28. *G. macrophylla***
- 82b. Fruit 3–7(–8) cm long _____ 83
- 83a. Fruit strongly constricted between the valves _____ **43. *G. aguilarii***
- 83b. Fruit not constricted between the valves _____ 84
- 84a. Ovary locules 9–12, petals c.17 mm long, fruit c.7.5 cm long, pyriform _____ **32. *G. carapoides***
- 84b. Ovary locules 4–8, petals 8–12 cm long, fruit usually 2.5–5.2 cm long, globose, botuliform, obovoid or pyriform _____ 85
- 85a. Fruit globose to shortly pyriform, valves 1-seeded _____ **37. *G. gomma***
- 85b. Fruit obovoid to shortly botuliform, valves 2-seeded _____ **39. *G. purusana***

1. *Guarea silvatica* C.DC. in Mart., Fl. Bras. 11(1): 195, t. 57 (1878); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 323, fig. 67 (1981). – Type: Brazil, Amazonas, ‘*in sylvis Japurensibus*’, fl., *Martius* s.n. (holo M). **Fig. 48A.**

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 324 (1981).

Abbreviated description. Young shoots and inflorescences minutely puberulous or glabrous, leaves paripinnate without a terminal bud, leaflets 2–4(–6) pairs, (6.5–)10–20(–32) × (2.5–)4–8(–13) cm, usually elliptic, less frequently lanceolate, oblanceolate or oblong-elliptic, chartaceous to thinly coriaceous, glabrous. Inflorescence axillary, or several on a short lateral shoot, 8–40(–125) cm long, unbranched, flowers clustered along the axis in distant cymose fascicles, petals 4(–5), imbricate, 5–7.5(–10) mm long, staminal tube (4–)5–6(–8.5) mm long, 1.5–3 mm broad, anthers (5–)8(–10),

ovary 2–3(–4)-locular, locules with 1–2 superposed ovules, capsule 3.8–5 cm long, 2.5–4 cm broad, constricted between the seeds, smooth, glabrous, 2(–3)-valved, pericarp 1.5–2 mm thick, valves 1-seeded. Seed coat bony, c.1 mm thick, cotyledons collateral.

Distribution and ecology. Southern Venezuela and the Guianas, Amazonian Colombia, Ecuador and Peru, and Amazonian Brazil. Mostly a component of primary lowland rain forest on non-flooded land. Its ability to sucker from cut trunks enables it to persist in secondary regrowth, where it may flower as a small treelet.

Representative additional collections. COLOMBIA. **Caquetá:** Solano, 8 km SE of Tres Esquinas (NW0075), *Little & Little* 9702 (K).

VENEZUELA. **Amazonas:** San Carlos de Rio Negro (NW0167), *H.L. Clark* 7237 (K).

GUYANA. Upper Takutu-Upper Essequibo Region, Acarai Mts. (NW0158), *D. Clarke et al.* 7577 (K).

SURINAM. Tumuc Humac Mts., Talouakem (NW0254), *Acevedo-Rodriguez et al.* 5986 (K).

FRENCH GUIANA. Vicinity of Les Eaux Claires, 6 km NNW of Saül (NW0353), *N.P. Smith et al.* 13 (K).

ECUADOR. **Morono-Santiago:** 40 km NNE of Macas (SW0278), *Pennington & Tenorio* 10797 (K). **Napo:** 8 km below Misahualli, Jatun Sacha (SW0177), *Palacios & Neill* 958 (K). **Orellana:** Yasuní National Park, Maxus road km 8–10 (SW0076), *Zuleta* 128 (K). **Zamora-Chinche:** Quimi Valley (SW0378), *van der Werff et al.* 19177 (K).

PERU. **Loreto:** Maynas, R. Itaya, San Antonio (SW0373), *Vásquez & Jaramillo* 3549 (K).

BRAZIL. **Acre:** Município Mal. Traumaturgo, Rio Alto Jurua, N of São João do Breu (SW0972), *Silveira et al.* 524 (K). **Amazonas:** Manaus, Ducke Reserve (SW0259), *Assunção et al.* 328 (K). **Pará:** Marabá, Carajas (SW0549), *Maciel et al.* 799 (K).

The ITS phylogeny indicates that *Guarea silvatica* occupies a very isolated position at the end of a long, basally divergent branch. Morphologically it is anomalous in having leaves lacking the terminal bud, imbricate petals and seeds with a bony seed coat and embryo with collateral cotyledons. However, it retains the essential characters of the genus (stamens inserted within the throat of a complete staminal tube and the stipitate ovary with discoid style-head).

2. *Guarea anomala* T.D.Penn., sp. nov. [T.D.Penn., Bol. Técn. Centro Pesq. Cacao 143: 21, fig. 11 (1986), nom. inval. (in Portuguese)]. **Figs 3, 51A.**

A speciebus aliis foliolis alternis, uno foliolo paris ultimis ad instar folioli terminalis ordinato, inflorescentia minuta, floribus glabris, petalis 3–4, ovario 3–4-loculare distinguenda. – Type: Brazil, Bahía, Município de Ilheus, road between Sururu and Vila Brasil, 6–14 km from Sururu, 12–20 km SE of Buerarema [SW1439], 100 m altitude, fl., *Mori & Benton* 12995 (holo CEPEC; iso K, NY, RB, US).

Young shoots slender, shortly pubescent at first, soon glabrous, becoming pale whitish, smooth or slightly scaling, without lenticels, 5–6 mm diam. *Leaves* pinnate with one leaflet orientated to simulate a terminal leaflet, petiole 2.8–6.1 cm long, slender, semiterete, glabrous, rhachis 7–11 cm long, terete; petiolule 0.7–1.2 cm long, pulvinate at the base, the pulvinus transversely corrugated, glabrous. *Leaflets* 5–6,

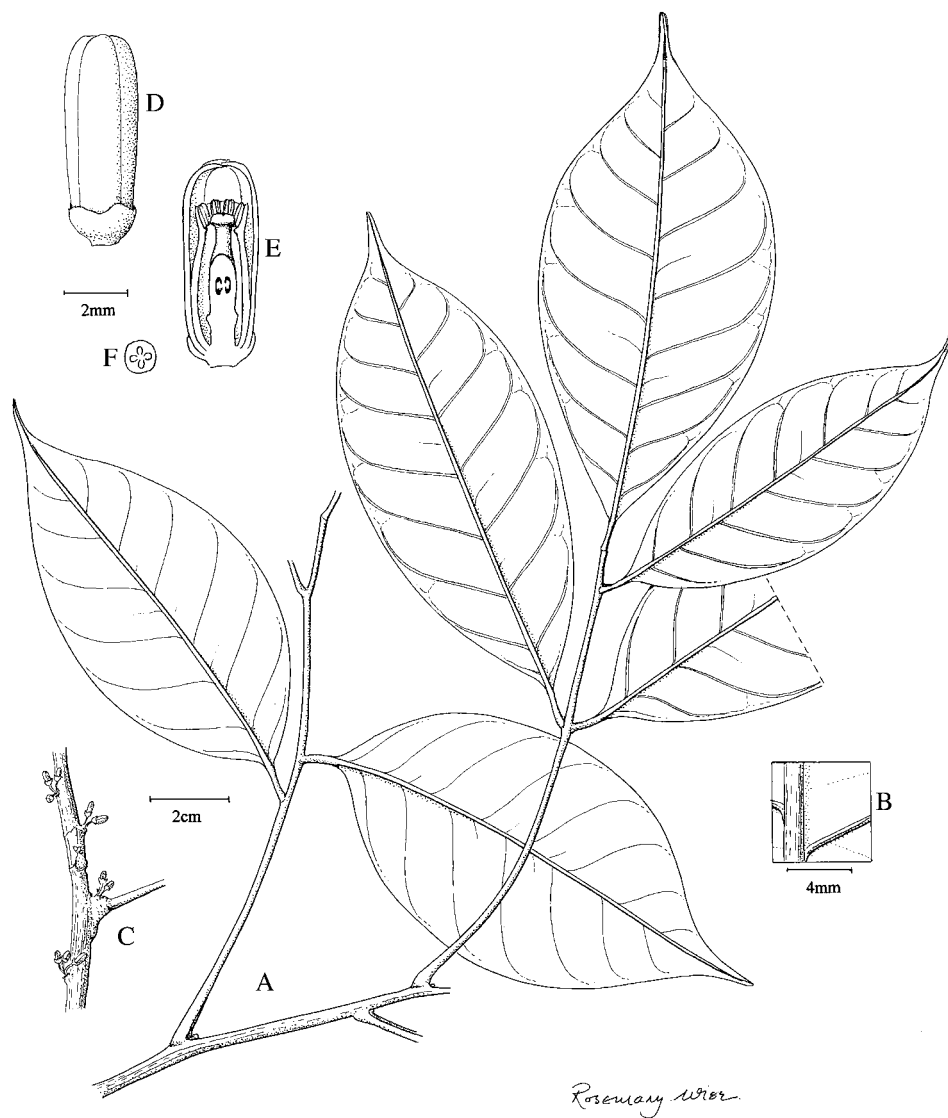


FIG. 3. *Guarea anomala* T.D.Penn. A, habit; B, enlargement of leaf undersurface; C, inflorescences; D, flower; E, half-flower; F, cross-section of ovary. (A–F, Mori & Benton 12995).

alternate or rarely a few opposite, largest (uppermost) up to 17×7.1 cm, smallest (lowermost) $c.6.5 \times 4.1$ cm, elliptic, apex narrowly attenuate, thinly coriaceous, glabrous, not glandular-punctate or -striate; venation eucamptodromous, midrib slightly raised on the upper surface, secondaries 9–11 pairs, ascending, slightly arcuate, slightly convergent, intersecondaries moderately long, tertiaries obscure. *Inflorescence* axillary or on twigs below the leaves, $c.1$ cm long, a few-flowered

fascicle, indumentum of a few appressed hairs; pedicel c.1 mm long. *Calyx* cup-shaped, c.1 mm long, with 3–4 minute shallow teeth, glabrous. *Petals* 3–4, 6–7 mm long, c.1.5 mm broad, strap-shaped, apex acute, aestivation valvate or slightly imbricate, glabrous. *Staminal tube* c.5 mm long, c.1.5 mm broad, margin undulate, glabrous; anthers 8, c.1 mm long, oblong, dehiscent, glabrous. *Nectary* c.1.5 mm long, a stout stipe expanded at the apex into a collar below the ovary, glabrous. *Ovary* 1.5–2 mm long, slender, 3–4-locular, locules with 1 ovule, glabrous, style c.1 mm long, stout, glabrous, surmounted by a thick discoid stigma. *Fruit* unknown.

Field characters. Tree to 15 m high and 25 cm diam., with reddish flowers. Flowering recorded in November and April.

Distribution and ecology. Known only from Bahía, Brazil where it is a component of the southern Bahian wet forest around 100 m altitude.

Collections examined. BRAZIL. **Bahía:** road Guaratinga to São Paulinho (SW1639), *Pinheiro* 2092 (CEPEC, K).

Local name. Cedro cabacinha.

Guarea anomala is a most distinctive species, unlike any other in the genus; indeed at first sight it appears to be a species of *Trichilia*. It has alternate leaflets, with the uppermost one orientated to simulate a terminal leaflet; it lacks the terminal bud characteristic of nearly all species in the genus; and the leaflets have a pulvinate, corrugated petiolule reminiscent of many legumes and lack higher order venation. The minute fasciculate inflorescence is also distinctive, as are the small flowers with 3–4 petals and 3–4-locular ovary. Of the 22 flowers studied, 9 have 3 petals and 13 have 4 petals.

The ITS phylogeny confirms its isolated position at the end of a long, basally divergent branch. Like *Guarea silvatica* it has retained the essential characters of the genus.

Note on species 3–9. These are all closely related members of the *Guarea glabra* complex, whose relationships are discussed in the Phylogenetics section above. There is little genetic or morphological variation between the component species, and their placement at the end of a long branch suggests an ancestral dispersal into Central America and a recent species radiation.

3. *Guarea gentryi* Coronado, *Novon* 16(4): 464 (2006). – Type: Costa Rica, Heredia, Finca la Selva, OTS Field Station, fl., *Folsom* 9404 (holo MO; iso CR, F). **Figs 4, 52A.**

Young shoots minutely appressed puberulous at first, soon glabrous, becoming greyish brown, smooth with a few large lenticels, 5–8 mm diam. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 4.5–7.5 cm long, semiterete, glabrous, rhachis 6.5–22 cm long, semiterete, glabrous; petiolule 5–12 mm long, minutely puberulous. *Leaflets* opposite, 2–3 pairs, uppermost 11.5–21.5 × 7–9 cm,



FIG. 4. *Guarea gentryi* Coronado. A, habit; B, enlargement of leaf undersurface; C, inflorescence; D, flower bud; E, half-flower; F, infructescence. (A-C, *Fuchs & Zanella* 22361; D-F, *Hammel et al.* 17058).

lowermost 8–14 × 5–6.7 cm, broadly elliptic to obovate or oblong-elliptic, apex shortly acuminate to obtusely cuspidate, base narrowly cuneate or attenuate to acute, coriaceous, upper surface glabrous, lower surface sparsely and minutely appressed puberulous, with scattered minute red papillae and small tufts of hairs in the axils of the secondary veins, not glandular-punctate or -striate; venation eucamp-todromous, midrib slightly sunken on the upper surface, secondaries 8–10 pairs, ascending, slightly arcuate and slightly convergent, intersecondaries absent, tertiaries oblique, parallel; higher order venation obscure. *Inflorescence* axillary or on twigs below the leaves, 10–19 cm long, a profusely branched panicle, branches perpendicular to steeply ascending, the lower ones up to 10 cm long, minutely appressed puberulous, bracts c.1 mm long, navicular, ovate; pedicel c.1 mm long. *Calyx* patelliform, 0.5–0.75 mm long, with 4 shallow irregular lobes or teeth, appressed puberulous outside, glabrous inside. *Petals* 4(–5), 3–4 mm long, 1–1.5 mm broad, strap-shaped to lanceolate, apex acute, free, valvate, appressed puberulous outside, glabrous inside. *Staminal tube* c.2.5 mm long, 1.5–2.5 mm broad, margin undulate, glabrous; anthers 8, 0.6–0.8 mm long, oblong, dehiscent, glabrous. *Nectary* absent, but ovary on a short, stout stipe. *Ovary* 0.75–1 mm long, ellipsoid to ovoid, 4-locular, locules with 1 ovule, glabrous, style 0.5–0.75 mm long, style-head discoid. *Fruit* c.2.5 × 3 cm, broadly pyriform, apex truncate, base cuneate to obtuse, 4-valved, valves 1-seeded, rather rough-skinned, glabrous, brown, pericarp 3–5 mm thick. *Seed* 1.5–2 cm long.

Field characters. Tree to 30 m high and 1 m diam., bark scaling in large patches, greyish, flowers greenish white. Flowering February to March in Colombia, recorded in March and June in Costa Rica and Nicaragua.

Distribution and ecology. In lowland rain forest below 500 m altitude, in Colombia (Choco), Panama, Costa Rica and Nicaragua.

Collections examined. NICARAGUA. **Zelaya:** 60 km NW of Puerto Cabezas, S of R. Wawa (NW1483), *Little* 25202 (MO); *Kurinwacito* (NW1384), *Moreno* 23640 (K, NY), 23685 (K), 23708 (K).

COSTA RICA. **Heredia:** Braulio Carillo National Park, Magsasay Station (NW1084), *Acevedo-Rodríguez et al.* 150 (INB, K, MO), *Gentry* 71760A (K); Braulio Carillo National Park, El Ceibo Station (NW1084), *Aguilar & Hammel* 35 (CR, MO); PN Braulio Carillo, Puesto el Ceibo (NW1084), *Boyle* 1394 (K), *Boyle & Ezeta* 2800 (CR); Finca la Selva, OTS Station (NW1084), *Hammel & Trainer* 12844 (F, MO, NY), *Hartshorn* 1408 (MO); PN Braulio Carillo, Magsasay (NW1085), *Carballo* 157 (INB, K); La Selva Rio Sarapiquí (NW1084), *Gentry et al.* 78629 (K). **Limón:** Canton de Talamanca, Amubri (NW0982), *Hammel et al.* 17515 (CR); Reserva Forestal Cordillera Volcanica Central (NW1083), *Hammel et al.* 17058 (F, K); Matina, PN Barbilla, Colonia Puriscalina (NW0983), *Mora* 906 (CR, INB).

PANAMA. **Colon:** Santa Rita (NW0979), *Correa & Dressler* 735 (NY).

COLOMBIA. **Choco:** area of Baudo, R. Baudo, 19 km upstream from estuary (NW0477), *Fuchs & Zanella* 22361 (COL, G, K, NY, US).

Local name. Charde (Colombia) (possibly a corruption of Chalde which is used in Colombia for other *Guarea* species).

This species is clearly closely related to *Guarea glabra*, sharing with it the hair tufts in the axils of the secondary veins and small 4-merous flowers with glabrous ovary. It differs in the minute whitish appressed indumentum on the lower leaflet surface, in the profusely branched inflorescence and very small flowers. The leaves dry brown on both surfaces.

The Colombian specimens were recognised as a new species (on herbarium sheets) many years ago, but only recently was complete material obtained from Costa Rica.

4. *Guarea bijuga* C.DC. in A.DC. & C.DC., Monogr. Phan. 1: 567 (1878). – Type: Guatemala, without exact locality, fl., *Skinner* s.n. (holo K). **Figs 5, 57A.**

Guarea erythrocarpa C.DC., Bull. Herb. Boissier, Sér. 2, 5: 420 (1905). – Type: Costa Rica, Cartago, Tucurrique, fl., fr., *Tonduz & Pittier* 13112 (holo G; iso BM, CR, F, G, GH, K, M, US, W, photo NY).

Guarea cook-griggsii C.DC., Smithsonian Misc. Collect. 68(6): 2 (1917). – Type: Guatemala, Alta Verapaz, near Finca Sepacuite, fl., *Cook & Griggs* 408 (holo US; photo NY).

Guarea matudai Lundell, Lloydia 2: 93 (1939). – Type: Mexico, Chiapas, Mt. Tacana, fl., *Matuda* 2449 (holo MICH n.v.; iso A, F, K, MEXU, NY, US).

Guarea glabra auct. non Vahl: T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 268 (1981), p.p.

Young shoots 4–6 mm diam., puberulous at first, soon becoming glabrous, greyish buff, smooth, with some large lenticels. *Leaves* pinnate with an active terminal bud, petiole 4–9(–14) cm long, semiterete at first, becoming terete with age, glabrous, rhachis 4–25 cm long, semiterete to slightly channelled, glabrous; petiolule stout, 5–10 mm long, glabrous. *Leaflets* opposite, up to 4 pairs, (10.3–)15–25(–38) × (4.2–)6.7–10(–12) cm, broadly elliptic or oblong-elliptic, apex acuminate to obtusely cuspidate, base obtuse, narrowly cuneate, acute or narrowly attenuate, thinly coriaceous, glabrous, drying pale green, not glandular-punctate or -striate; venation eucamptodromous, midrib slightly sunken on the upper surface, secondaries (6–)7–11(–12) pairs, steeply ascending, straight or slightly arcuate, parallel to slightly convergent, intersecondaries short or absent, tertiaries oblique, parallel. *Inflorescence* axillary or on small twigs below the leaves, 4–15 cm long, a raceme or narrow thyrses, unbranched or with short lateral branches to 3 cm long, glabrous; pedicel 2–4 mm long, glabrous. *Flowers* unisexual (plant dioecious). *Calyx* (1–)2–3 mm long, patelliform or shallowly cup-shaped with 4 shallow to deep lobes, glabrous. *Petals* 4, male (6.5–)7–10 × 1.5–2.5 mm, female 6–7.5 × 1.5–2 mm, strap-shaped, apex acute, free, valvate, glabrous. *Staminal tube* (male) 5–8 × 2–3 mm, female 5–6 × 2–3 mm, broadly tubular, margin truncate or slightly undulate, glabrous; anthers 8(–9), 0.8–1 mm long, oblong, antherodes in female similar but not dehiscent. *Nectary* 0.5–1.5 mm long, a stout stipe slightly expanded into a collar at the base of the ovary. *Ovary* c.2 mm long, ovoid, 4-locular, locules 1-ovulate, glabrous, male with rudimentary ovules, style 3–5 mm long, glabrous, style-head discoid. *Capsule* 1.3–3 × 1.3–3 cm,

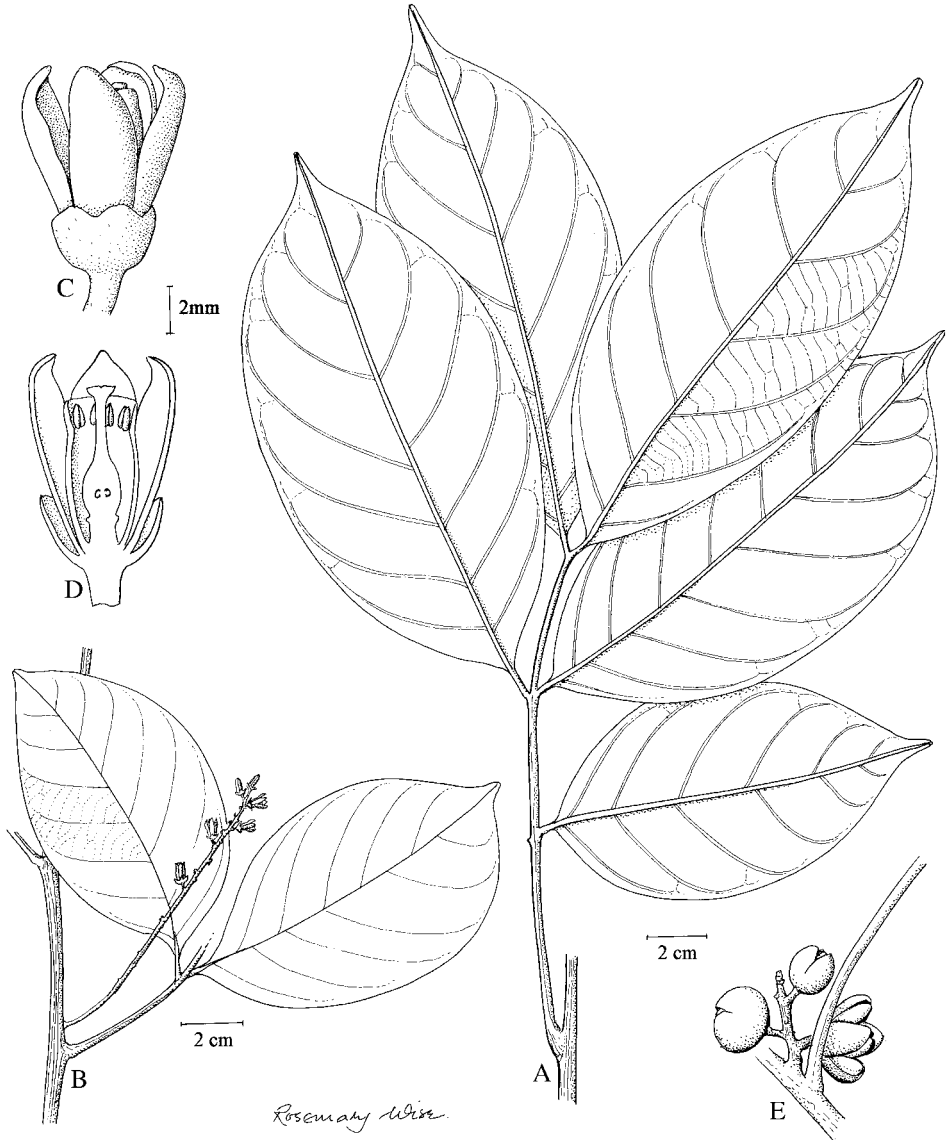


FIG. 5. *Guarea bijuga* C.DC. A, leaf; B, inflorescence; C, flower; D, half-flower; E, infructescence. (A, *Hawkins* 1221; B–D, *Bello* 4621; E, *Marshall et al.* 418).

globose, apex and base obtuse to truncate, often slightly lobed when dry and constricted between the seeds, (3–)4-valved, pericarp c.1 mm thick, fleshy, rough-skinned and rather warty with numerous pale lenticels, glabrous. *Seeds* 2–4, 1–2.5 cm long, shaped like the segment of an orange or banana-shaped; embryo with thick plano-convex, superposed cotyledons, radicle abaxial, extending to the surface.

Field characters. Tree to 25 m high and 80 cm diam., but often flowering when less than 10 m high. Bark pale brown, slightly scaling or fissured, slash fragrant. Flowers creamish-white, sometimes tinged with pink, mature fruit red, containing 2–4 seeds completely surrounded by a bright red sarcotesta. In Mexico flowering is recorded from March to July, with fruit maturing during the same period. From Guatemala to Nicaragua flowering is from November to February with the fruit maturing in April, and from Costa Rica southwards to Ecuador the flowering is from January to March, with ripe fruit recorded from April to October.

Distribution and ecology. Caribbean drainage of Veracruz and Tabasco, Mexico to Panama and the Pacific coast of Ecuador; not recorded from El Salvador. It is a tree of wet lowland rain forest, wet montane forest and cloud forest with an altitudinal range from sea level to 2700 m.

Representative additional collections. MEXICO. **Chiapas:** Escuintla, Mt. Ovando (NW1592), *Matuda* 4168 (F, K, NY); Estación Biol. Chajul (NW1690), *Dominguez Vásquez* 666 (MEXU). **Tabasco:** Cerro de Campanas, E of Teapa (NW1792), *Conrad & Gallegos* 2856 (MO, NY). **Veracruz:** Bastonal-Sierra Santa Marta road, c.14 km E of Lake Catemaco (NW1895), *Gentry et al.* 32450 (K).

GUATEMALA. **Alta Verapaz:** between Chajmayle and Sebol (NW1589), *Steyermark* 45739 (F). **Izabal:** Santo Tomas de Castilla (NW1588), *Marshall et al.* 418 (K). **Petén:** Seamay (NW1689), *Contreras* 6675 (NY). **Quiche:** Nebaj (NW1590), *Skutch* 1685 (NY, US). **San Marcos:** Volcan Tacana, between Canjula and La Union Juarez (NW1592), *Steyermark* 36502 (F).

BELIZE. **Cayo:** above Raspaculo R. (NW1688), *Hawkins* 1221 (K). **Toledo:** southern Maya Mountains, Bladen Nature Reserve (NW1688), *Davidse & Holland* 36665 (K, MO).

HONDURAS. **Atlántida:** Tela, Lancetilla (NW1587), *McDougal et al.* 3314 (K). **Yoro:** Rio Guan Guan (NW1587), *Hawkins & Merello* 823 (K).

NICARAGUA. **Chontales:** 4 km NNW of Cuapa, Cerro Oluma (NW1285), *Nee* 28406 (K). **Yelapa:** Cano Montecristo, Las Benitas (NW1183), *Moreno* 15008 (K).

COSTA RICA. **Alajuela:** Monteverde Reserve, Rio Penas Blancas (NW1084), *Haber* 811 (K). **Cartago:** Turrialba, Tayutic, Grano de Oro (NW0983), *Cascante* 642 (CR, K). **Guanacaste:** Canton de la Cruz, Parque Nacional Guanacaste, Estación Maritza (NW1085), *Espinosa* 223 (K). **Heredia:** Sarapiquí, Puerto Viejo, Finca la Selva (NW1084), *Hartshorn* 1450 (F). **Puntarenas:** Canton de Osa, Rio Piedras Blancas (NW0883), *Aguilar et al.* 2259 (K).

PANAMA. **Bocas del Toro:** vicinity of Fortuna Dam (NW0882), *McPherson* 9725 (K). **Veraguas:** 5 miles W of Santa Fe (NW0881), *Liesner* 893 (MO).

ECUADOR. **Esmeraldas:** Eloy Alfaro, Mayronga (NW0079), *Pennington et al.* 14080 (K, QCNE). **Los Ríos:** Cerro Samana, Hacienda Clementina (SW0179), *Stahl* 6701 (K).

This species differs from *Guarea glabra* in its broader leaflets which lack the hair tufts in the axils of the secondary veins. Apart from a little indumentum on the youngest shoots, the plant is completely glabrous. In Central America where its range overlaps that of *Guarea glabra*, it also differs in having a slightly longer, shallowly cup-shaped calyx and in its slightly longer petals. However, in the Lesser Antilles *Guarea glabra* is morphologically almost identical with *G. bijuga*, the only difference being the presence of hair tufts in the vein axils of *G. glabra*. Another characteristic of *Guarea bijuga* is the tendency of the persistent calyx in specimens

with young fruit to develop a pale and slightly thickened margin. The leaves of *Guarea bijuga* nearly always dry pale green.

5. *Guarea luxii* C.DC. in J.D.Smith, Bot. Gaz. (Crawfordsville) 19: 2 (1894). – Type: Guatemala, Dept. Santa Rosa, Santa Rosa [NW1490], fl., *Heyde & Lux* 3276 (holo G; iso BM, G, K, photo NY). **Figs 6, 57B.**

Guarea glabra auct. non Vahl: T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 268 (1981), p.p.

Young shoots slender, 2–4 mm diam., finely puberulous at first, soon becoming glabrous, greyish white, smooth, with a few lenticels. *Leaves* pinnate with an active terminal bud, petiole 2–3.5 cm long, semiterete, sparsely appressed puberulous to glabrous, rhachis 2–16 cm long, semiterete, minutely puberulous to glabrous; petiolule 2–3 mm long. *Leaflets* opposite, up to 6 pairs, (5.6–)8–11.3(–14.5) × (1.5–)2.5–3.6(–4) cm, narrowly elliptic or oblanceolate, apex acuminate, base narrowly attenuate or cuneate, chartaceous, glabrous, drying green, sometimes slightly glandular-striate; venation eucamptodromous in the lower half, brochidodromous in the upper half, midrib sunken on the upper surface, secondaries 12–18 pairs, shallowly ascending, slightly arcuate and slightly convergent, intersecondaries usually frequent and extending to near the margin; higher order venation laxly reticulate. *Inflorescence* an axillary thyrses, 2–11 cm long, usually few-flowered, lower branches up to 3 cm long, sparsely puberulous; pedicel 2–4 mm long, puberulous. *Calyx* c.1 mm long, patelliform with 4 shallow acute to obtuse lobes, sparsely appressed puberulous outside, glabrous inside. *Petals* 4, male 5–6 × 1.5–2 mm, female 4.5 × 2 mm, strap-shaped, apex acute, free, valvate, with scattered minute appressed hairs outside, glabrous inside. *Staminal tube* (male) 4–4.5 × 1.5–2 mm, female 3.5 × 1.5 mm, tubular, margin undulate, glabrous; anthers 8, c.0.8 mm long, oblong, glabrous, antherodes in female similar but not dehiscent. *Nectary* c.1.5 mm long, a stipe slightly expanded into a collar below the ovary, shorter and unexpanded in the female. *Ovary* c.1.5 mm long, ovoid, 4-locular, locules 1-ovulate, glabrous, male with rudimentary ovules, style 1.5–2 mm long, glabrous, style-head discoid. *Capsule* 1.2–2.5 × 1.7–2.7 cm, obovoid to globose, apex rounded to truncate, base obtuse to truncate, often slightly lobed when dry and constricted between the seeds, (3–)4-valved, pericarp 0.5–1 mm thick, smooth, glabrous, sometimes lenticellate. *Seeds* 2–4, 1–2 cm long, shaped like the segment of an orange; embryo with thick plano-convex, superposed cotyledons, radicle abaxial, extending to the surface.

Field characters. Treelet 3–10 m high with whitish or cream flowers and reddish brown capsules; the seed is surrounded by a bright red or orange sarcotesta. Flowering has been recorded in January, March, May and August and mature fruit in January, February, April and June.

Distribution and ecology. Mexico (Chiapas), Guatemala and El Salvador, in cloud forest, with all collections between 1800 m and 2600 m altitude (except for the type collection *Heyde & Lux* 3276 which is annotated 3000 ft (c.900 m)).

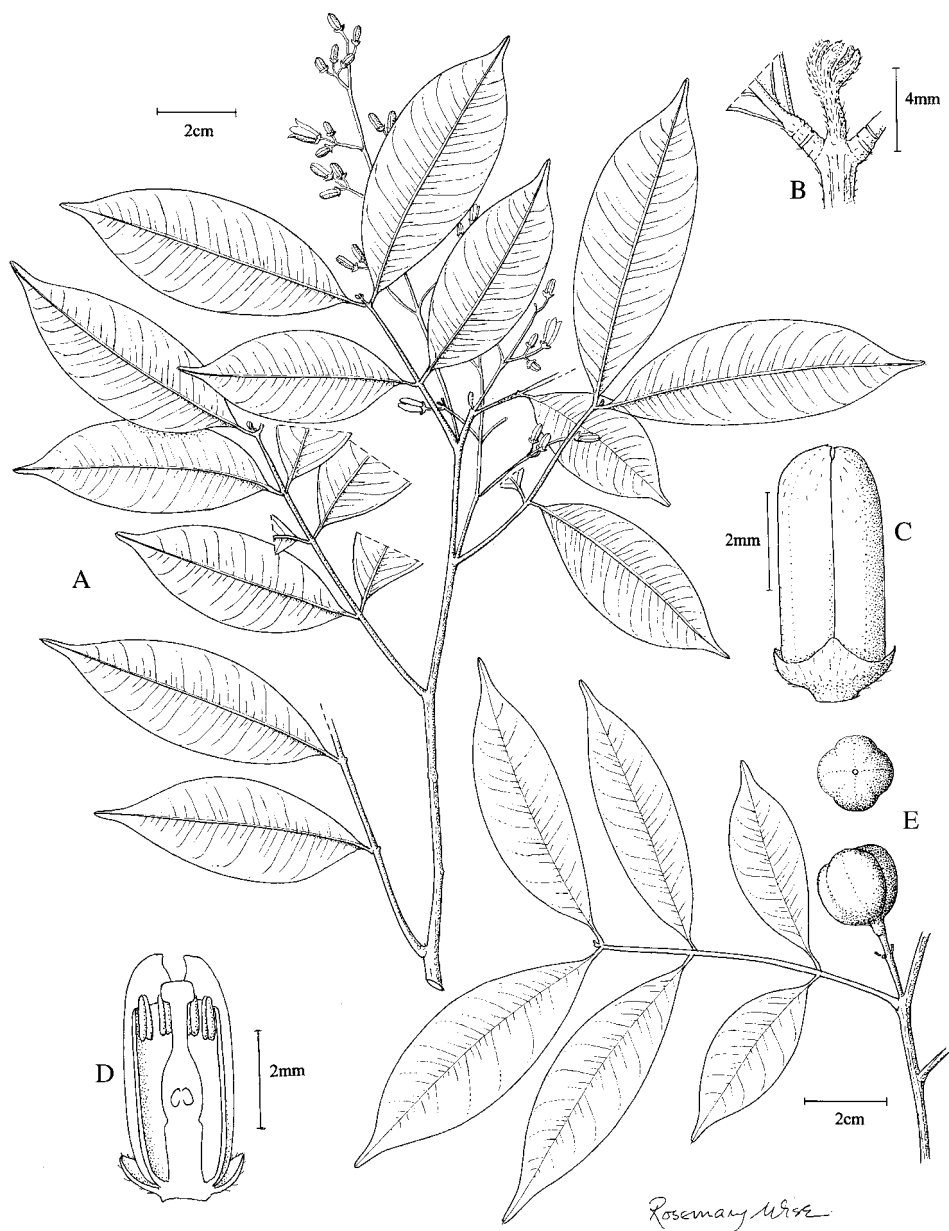


FIG. 6. *Guarea luxii* C.DC. A, habit; B, dormant bud at leaf apex; C, flower bud; D, half-flower; E, fruit. (A–D, Martinez s.n.; E, Villacorta & Lara 2650).

Collections examined. MEXICO. **Chiapas:** Escuintla, Santa Rosa (NW1490), *Matuda* 18660 (MEXU); Municipio La Concordia, El Triunfo Reserve (NW1592), *Hampshire et al.* 721 (G).

GUATEMALA. **Quetzaltenango:** above Mujalia, between San Martín Chile Verde and Colomba (NW1491), *Standley* 84898 (F); El Pocito, S of San Martín Chile Verde (NW1491), *Standley* 85046 (F).

EL SALVADOR. **Santa Ana:** Santa Ana, Montecristo National Park, Cordillera de Metapán (NW1489), *Davidse et al.* 37299 (K, MO); San José, Ingenio, Montecristo National Park (NW1489), *Martínez* s.n. (MO); Montecristo (NW1489), *Molina & Molina* 12634 (F, US), 12646 (F, NY); Cordillera Miramundo (NW1489), *Molina et al.* 16910 (NY); Cerro Miramundo, Montecristo National Park (NW1489), *Monterrosa* 186 (K, MO); Montecristo cloud forest (NW1489), *Reyna* 1454 (K); Miramundito, Montecristo National Park (NW1489), *Villacorta & Lara* 2650 (K, MO).

This species was treated as an informal ecological race of *Guarea glabra* in *Flora Neotropica* (Pennington *et al.*, 1981), but the recent availability of additional fertile material enables it to be restored here to species rank, a move supported by a recent unpublished numerical study (Coronado, 2003). It is very similar to *Guarea glabra* subsp. *excelsa*, but differs in the small slender leaflets with more numerous secondary veins, and it lacks the characteristic hair tufts in the vein axils. The species are identical in floral and fruit structure. *Guarea luxii* is confined to high altitude cloud forest, whereas *G. glabra* subsp. *excelsa* is a tree of tropical deciduous forest at low elevations.

- 6. *Guarea glabra*** Vahl, *Eclog. Amer.* 3: 8 (1807); T.D.Penn. in T.D.Penn. *et al.*, *Fl. Neotrop.* 28: 268 (1981). – Type: St. Croix, Montserrat, fl., *Ryan* s.n. (holo C).
Guarea ramiflora Vent., *Mem. Cl. Sci. Math. Inst. Natl. France* 1: 20 (1807); Vent., *Choix Pl. t.* 41 (1807). – Type: Puerto Rico, fl., Collector not cited (ex herb. Ventenat) s.n. (holo G).
Guarea swartzii DC., *Prod.* 1: 624 (1824). – Type: Without definite locality, *Forsyth* s.n. (lecto G-DC, designated by C. de Candolle, *Monogr. Phan.* 1: 563 (1878)).
Guarea humilis Bert. ex DC., *Prod.* 1: 624 (1824). – Type: Puerto Rico, fl., *Bertero* s.n. (holo G-DC; iso MO).
Guarea vahliana A.Juss., *Bull. Sci. Nat. Géol.* 23: 239 (1830); A.Juss., *Mém. Mus. Hist. Nat.* 19: 240, 282 (1831). – Type: Guadeloupe, fl., *Perrotet* s.n. (holo P).
Guarea schomburgkii C.DC. in A.DC. & C.DC., *Monogr. Phan.* 1: 565 (1878). – Type: Guyana, *Schomburgk* 779 (lecto G-DC, designated by Pennington in Pennington *et al.* (1981: 268); islecto G, K, NY, P).
Guarea pauciflora Sessé & Moc., *Fl. Mexic.* 100 (1894); Sessé & Moc., *Fl. Mexic.*, ed. 2, 92 (1894). – Type: Puerto Rico, mountains of Toa Alta, fl., *Sessé* s.n. (5117 in MA) (holo MA).
Guarea lherminieri C.DC., *Bull. Herb. Boissier* 2: 571 (1894). – Type: Guadeloupe, fl., *Lherminier* s.n. (holo G).
Guarea syringoides C.H.Wright, *Bull. Misc. Inform. Kew* 1906: 3 (1906). – Type: Ecuador, Manabi, El Recreo, fl., *Eggers* 15602 (lecto K, designated by Pennington in Pennington *et al.* (1981: 269); islecto BM, C, F, M, S, US).
Guarea ternifoliola C.DC., *Smithsonian Misc. Collect.* 68: 2 (1917). – Type: Panama, Chiriqui, Remedios, fl., *Pittier* 5466 (holo US; iso G (fragment), GH, NY).
Guarea obtusata Blake, *Proc. Biol. Soc. Washington* 33: 118 (1920). – Type: Mexico, Oaxaca, Cerro Espino, Cafetal Concordia, fl., *Reko* 3701 (holo US; iso MEXU).
 This plant is intermediate with *Guarea glabra* subsp. *excelsa*.

Guarea microcalyx Harms, Notizbl. Bot. Gart. Berlin-Dahlem 9: 429 (1925). – Type: Ecuador, Manabi, El Recreo, fl., *Eggers* 15602 (holo B, destroyed; lecto BM, designated here; isolecto C, F, M, P, S).

Guarea ciliata Al.Rodr., Lankesteriana 6: 105 (2006), **syn. nov.** – Type: Costa Rica, Heredia, La Virgen, La Selva Biological Station, fr., *Rodríguez* 8400 (holo INB; iso CR).

Young shoots 3–5 mm diam., appressed puberulous at first, soon glabrous, becoming pale greyish-buff, smooth, with some raised lenticels. *Leaves* pinnate with an active terminal bud, petiole 2–6 cm long, semiterete, appressed puberulous at first, soon glabrous, rhachis up to 30(–50) cm long, semiterete to terete, appressed puberulous at first, becoming glabrous and later woody with age; petiolule 2–6 mm long, subglabrous. *Leaflets* opposite, up to 8 pairs, (6.5–)10–16(–25) × (2.5–)3–6(–9.5) cm, usually narrowly to broadly elliptic or oblanceolate, occasionally oblong-elliptic, apex acuminate to obtuse or obtusely cuspidate, occasionally rounded, base narrowly attenuate, cuneate or acute, chartaceous to thinly coriaceous with tufts of hair in the axils of the secondary veins on the lower surface, otherwise glabrous (subsp. *glabra*, *excelsa*, *microcarpa*, *tuerckheimii*) or with some pubescence below (subsp. *glabrescens*, *rovirosae*), often obscurely glandular-punctate and -striate; venation eucamptodromous, midrib flat or slightly sunken on the upper surface, secondaries 6–10(–16) pairs, ascending, moderately to strongly arcuate, convergent, intersecondaries usually absent, tertiaries perpendicular to oblique, sometimes close and parallel, and sometimes reticulate. *Inflorescence* axillary, or sometimes on older wood below the leaves, (1–)5–15(–25) cm long, a panicle with short lateral branches usually not more than 5 cm long, ultimate branches racemose or cymose, sparsely appressed puberulous to subglabrous; pedicel 1–3 mm long, sparsely appressed puberulous to glabrous. *Calyx* 0.75–2(–2.5) mm long, patelliform to shallowly cup-shaped, margin usually shallowly 4-lobed, occasionally truncate, with sparse indumentum or glabrous outside, glabrous inside. *Petals* 4(–5), 4–9 × 1.5–2.5 mm long (see note below on dimensions of male and female flowers), strap-shaped, apex acute, sparsely appressed pubescent to glabrous outside, glabrous inside. *Staminal tube* 2.5–7.5 × 1.5–3 mm, broadly tubular to ± globose, margin undulate or shallowly toothed, nearly always glabrous, rarely with sparse appressed hairs outside; anthers (7–)8(–10), 0.75–1 mm long, oblong, glabrous, antherodes in female similar but without pollen and not dehiscent. *Nectary* 0.5–2 mm long, a stipe expanded into a collar below the ovary, glabrous, in female shorter and unexpanded. *Ovary* 1–2.5 mm long, ovoid, 4(–5)-locular, locules 1-ovulate, glabrous, male with rudimentary ovules, style 1–2 mm long, glabrous, style-head discoid. *Capsule* (1–)1.4–2.5(–3) × (1.4–)1.6–2.5(–3) cm, usually broader than long, ± globose, apex rounded to truncate, base obtuse, rounded or truncate, (3–)4-valved, pericarp 1–2 mm thick, smooth to rough and densely scurfy, glabrous. *Seeds* up to 4, (0.8–)1.2–2.2 cm long, shaped like the segment of an orange; embryo with thick plano-convex, superposed to oblique cotyledons, radicle abaxial, included or extending to the surface.

Note. *Guarea ciliata* Al.Rodr. is morphologically very similar to *G. ternifoliola* C.DC. (also a synonym of *Guarea glabra* subsp. *glabra*), with the same floral and fruit structure as typical *G. glabra*, but with the rather slender leaflets drying pale green, and with the axillary hair tufts reduced to a few hairs or absent. The young leaves on some specimens have a ciliate margin, but the mature leaflets are glabrous.

At any particular locality, there may be significant differences in the size of male and female flowers of this species, generally with the male flower having petals and staminal tube 1–2 mm longer than the female. However, across the range of the species these differences become obscured. Mexican material of the species is small-flowered, with the petals of both sexes not exceeding 4–6 mm long, but in Central America the flowers are larger, and the petals of female flowers from Guatemala, Nicaragua and Costa Rica are of equal length to or longer than those of male flowers from Mexico.

Field characters. Tree to 25 m high and 45 cm diam., often flowering when less than 10 m high, bark shallowly fissured or scaling, grey to grey-brown. The species is evergreen, even where it occurs in tropical deciduous forest. The flowers are white or whitish-green and fragrant, and the fruit matures from brown, through red to reddish purple. The inner face of the pericarp is white which contrasts with the bright reddish or orange sarcotesta which surrounds the seed. Flowering in the strongly seasonal climate along the Pacific drainage of Mexico and Central America occurs at the end of the dry season and beginning of the wet season from March to July, with the fruit maturing in the middle of the following dry season (February to March). In wet forest throughout the rest of its range, flowering has been recorded throughout the year.

Distribution. Mexico and Central America to northern South America, Pacific drainage of Ecuador, Amazonian Brazil south to Peru and Bolivia, Greater Antilles (Jamaica, Hispaniola and Puerto Rico), Lesser Antilles (Leeward and Windward Is.).

6a. *Guarea glabra* subsp. *glabra*. Figs 7, 62.

Young shoots and inflorescences appressed puberulous to glabrous, leaves glabrous (except for hair tufts), leaflets mostly elliptic, apex acute to acuminate, secondary veins mostly 6–10 pairs, arcuate, tertiary veins oblique, leaves drying green, petals mostly 5.5–8 mm long, glabrous, ovary glabrous.

Distribution and ecology. Same range as the species, except not yet recorded from Honduras, Belize and French Guiana. A tree of lowland and montane rain forest with a wide altitudinal range from near sea level to 1800 m. Occasionally found in drier areas, but then confined to damp ravines and water courses. In El Salvador it is confined to cloud forest at 800–1800 m altitude. Along the Amazonian flank of the Andes its altitudinal range is from 200 m to 600 m, in Jamaica up to 1500 m.

Representative additional collections. MEXICO. **Oaxaca:** Distrito Ixtlan, Rio Soyolapan watershed (NW1796), Boyle *et al.* 3896 (K).

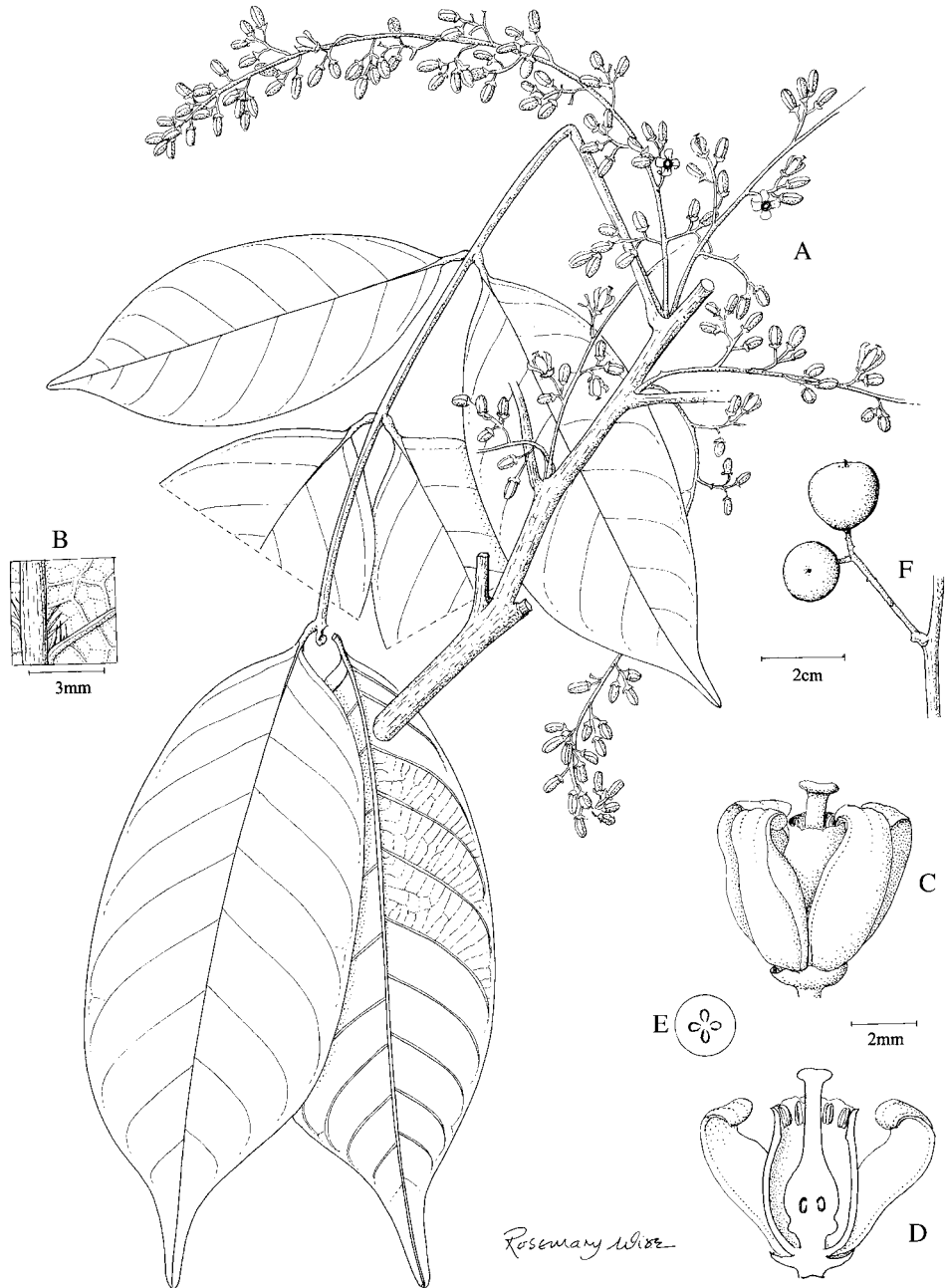


FIG. 7. *Guarea glabra* Vahl subsp. *glabra*. A, habit; B, enlargement of leaf undersurface; C, flower; D, half-flower; E, cross-section of ovary; F, fruit. (A–E, LBB 16283; F, BW 6677).

GUATEMALA. **Baja Verapaz**: Niño Perdido, San José (NW1590), *Lundell & Contreras* 21141 (MO, NY). **Sacatepequez**: SE of Alotenango, near Barranco Hondo (NW1490), *Standley* 64991 (F). **Solola**: between Patulul and San Lucas Toliman (NW1491), *Forther* 10257 (W).

EL SALVADOR. **Ahuachapan**: Municipio San Francisco Menendez, Cerro Davila (NW1389), *Sandoval & Chinchilla* 10 (K, MO). **La Libertad**: Laderas Sur del Plan de la Laguna (NW1389), *Lopez* s.n. (K, MO). **La Paz**: Zacatecoluta (NW1388), *Calderón* 324 (NY). **Santa Ana**: Montecristo National Park (NW1489), *Monterrosa et al.* 177 (MO). **Sonsonate**: Sierra Apaneca, Cerro el Pilón (NW1389), *Molina & Montalvo* 21611 (F).

NICARAGUA. **Río San Juan**: Río San Juan between El Tambor and Remolinos (NW1084), *Rueda et al.* 1903 (MO).

COSTA RICA. **Cocos Islands**: between Wafer and Cerro Iglesias, *Foster* 4120 (CR, K). **Heredia**: La Selva Biological Station, confluence of R. Sarapiquí and R. Puerto Viejo (NW1084), *Chaverri* 287 (INB, MO). **Limón**: Bribri (NW0982), *Gomez et al.* 20382 (MO). **Puntarenas**: Esparza, Macarona, Finca de José V. Herrera (NW0984), *Gomez* 20711 (K).

PANAMA. **Bocas del Toro**: above Chiriquí Grande (NW0882), *McPherson* 10472 (K, MO). **Canal Zone**: Madden Forest Reserve (NW0979), *Woods & Gallegos* s.n. (F, MO). **Chiriquí**: W of San Bartolo Limite (NW0882), *Croat* 22184A (MO). **Los Santos**: W of Tonosi (NW0780), *Holdridge* 6226 (MO). **Panama**: between El Llano and R. Mamon (NW0978), *Duke* 5627 (MO).

JAMAICA. **Clarendon**: Spaldings to Thompson Town, Bird Cave Rock (NW1877), *Acevedo-Rodríguez* 9654 (K, US). **Portland**: Marce's Gap towards Vinegar Hill (NW1876), *Anderson & Sternberg* 3471 (US). **St. Andrew**: Bellevue Peak, 2 miles W of Cinchona Botanic Garden (NW1876), *Kapos* 1583 (K, NY). **St. Thomas**: near Portland Gap (NW1876), *Proctor* 24023 (NY). **Trelawny**: 5.3 miles N of Quickstep Postal Agency (NW1877), *Thorne & Proctor* 48229 (NY).

DOMINICAN REPUBLIC. Pílancon, Bayaguana (NW1969), *A. & P. Liogier* 18883 (NY).

PUERTO RICO. Caribbean National Forest, El Verde Research Station (NW1865), *Boom* 10056 (K).

VIRGIN ISLANDS (USA). **St. Croix**: Montserrat (NW1764), *Ryan* s.n. (C).

LEEWARD ISLANDS. **Guadeloupe**: N of Trois Rivières (NW1661), *Jeremie* 888 (K). **Montserrat**: Centre Hills (NW1662), *J.S. Beard* 410 (K, MO). **Nevis**: Dos d'ane peak (NW1762), *J.S. Beard* 463 (K).

WINDWARD ISLANDS. **Dominica**: vicinity of Jean, NE of Salisbury (NW1561), *Ernst* 1818 (F, K). **Martinique**: Bois Gros, Morne du Lorrain (NW1460), *Duss* 591/4533 (NY). **St. Lucia**: Gros Piton (NW1360), *P. Beard* 1165 (MO). **St. Vincent**: without exact locality (NW1361), *Rev. L.G.* s.n. (K).

COLOMBIA. **Antioquia**: Parque National Natural 'Las Orquideas' Sector Galles (NW0676), *Cogollo et al.* 2653 (MO).

VENEZUELA. **Bolívar**: Altiplanicie de Nuria, 45 km N of Tumeremo, vicinity of Deborah (NW0761), *Steyermark* 89059 (K). **Falcon**: 20 km W of Tucacas (NW0968), *Cardozo & Wingfield* 190 (K). **Tachira**: Palo Grande to Minas de Carbon (NW0772), *Marcano-Berti & Sanchez* 982-065 (K). **Yaracuy**: Distrito San Felipe, 10 km N of Salom (NW1068), *Steyermark & Espinoza* 123802 (K).

TOBAGO. Parrot Hill (NW1160), *Broadway* 4562 (MO).

TRINIDAD. Bush Bush Forest, Nariva Swamp (NW1061), *Aitken* 18197 (K).

GUYANA. Pomeroon River, Arunamai Creek (NW0758), *FDBG* 2527 (K).

SURINAM. Brownsberg, Brokopondo District (NW0455), *LBB* 16283 (NY).

ECUADOR. **Cañar**: near Bucay (SW0279), *Camp* 3680 (NY). **Esmeraldas**: Timbre (NW0079), *Fagerlind & Wibom* 2492 (US). **Guayas**: Guayaquil, Cerro Blanco (SW0280), *Nuñez & Yagual* 249 (MO). **Manabí**: 10 km NE of Jama, Hacienda Don Juan (SW0080), *Neill et al.* 11672 (K).

Pastaza: Canton Pastaza, Pozo Petrolero ‘Moretecocha’ de ARCO (SW0177), *Gudiño et al.* 861 (K).

PERU. **Loreto:** Distrito Nauta, R. Marañon, Quebrada de Sapira (SW0473), *Rimachi* 4461 (K). **Madre de Dios:** Tambopata Reserve, R. Tambopata (SW1269), *Gentry & Young* 31829 (K).

BRAZIL. **Acre:** Municipio Santa Rosa, R. Purus, Seringal Mamuria (SW0969), *Daly et al.* 10064 (K). **Amapá:** Rio Araguari (NW0151), *J.M. Pires et al.* 50575 (K, NY). **Pará:** Macau airstrip, R. Maicuru (SW0054), *Strudwick et al.* 3419 (K). **Rondonia:** Municipio Porto Velho 13 km from Vila Campo Novo (SW1063), *Cid Ferreira* 8930 (K, US). **Roraima:** vicinity of Auaris (NW0464), *Prance et al.* 9850 (K).

BOLIVIA. **Pando:** Limoeiro (SW1169), *Carballal & Cardiel* 156 (K).

6b. *Guarea glabra* subsp. *excelsa* (Kunth) T.D.Penn., stat. nov. – *Guarea excelsa* Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 7: 227 (1825). – Type: Mexico, between Acapulco & Zumpango, fl., *Bonpland* s.n. (holo P). **Fig. 57C.**

Guarea fulva Triana & Planch., Ann. Sci. Nat. Bot. Ser. 5, 15: 371 (1872). – Type: Colombia, La Mesa, fr., *Triana* 3359 (holo P; iso BM, K).

Guarea purpurea C.DC. in A.DC. & C.DC., Monogr. Phan. 1: 564 (1878). – Type: [Peru] Mexico, fl., *Pavon* s.n. (holo K).

Guarea filiformis C.DC. in A.DC. & C.DC., Monogr. Phan. 1: 566 (1878). – Type: Mexico, Oaxaca, fl., *Jurgensen* 199 (lecto K, designated by Pennington in Pennington *et al.* (1981: 268); isolecto G).

Guarea filiformis C.DC. var. *pallida* C.DC., Monogr. Phan. 1: 566 (1878). – Type: Nicaragua, between Sapoá and Tortuga, fl., *Oersted* s.n. (herb. no. 80a in C) (holo C; iso F (fragment), photo NY).

Guarea filiformis C.DC. var. *cinerascens* C.DC. in A.DC. & C.DC., Monogr. Phan. 1: 567 (1878). – Type: Mexico, Morelos, Cuernavaca, fl., *Bourgeau* 1197 (holo K; iso P).

Guarea palmeri N.E.Rose ex C.DC., Bot. Gaz. (Crawfordsville) 19: 39 (1894). – Type: Mexico, Colima, Manzanillo, fr., *Palmer* 1391 (holo G; iso GH, K, NY, US).

Guarea virescens C.DC., Annuaire Conserv. Jard. Bot. Geneve 10: 140 (1907). – Type: Mexico, Guerrero, banks of R. Coayaquilla, fl., fr., *Langlássé* 917 (holo G; iso GH, K, NY, P, US, photo NY).

Guarea makrinii Blake, Contr. Gray Herb. n.s. 53: 57 (1918). – Type: Mexico, Oaxaca, Pochutla, fl., *Conzatti, Reko & Makrinus* 3244 (holo GH; iso MEXU).

Guarea excelsa Kunth var. *dubia* Blake, Proc. Biol. Soc. Washington 34: 116 (1921). – Type: Mexico, Nayarit, Tres Marias Is., fl., *Nelson* 4230 (holo US; iso A, F, GH).

?*Guarea chiapensis* Blake, Proc. Biol. Soc. Washington 34: 116 (1921). – Type: Mexico, Chiapas, Finca Irlanda, fl., *Purpus* 7374 (holo US; iso GH, MO, NY).

Guarea polyantha Blake, Proc. Biol. Soc. Washington 34: 117 (1921). – Type: Mexico, Guerrero, near Acapulco, fl., *Palmer* 578 (holo US; iso A, F, GH, K, MO, NY).

Guarea heterophylla Blake, Proc. Biol. Soc. Washington 34: 116 (1921). – Type: Mexico, Oaxaca, Pinotepa, fl., *Galeotti* 7247D (holo US; iso F, G, GH, NY, photo NY).

Young shoots and inflorescences appressed puberulous to glabrous, leaves glabrous (except for hair tufts), leaflets mostly oblanceolate, apex obtuse to acute or acuminate, secondary veins 6–10 pairs, arcuate, tertiary veins reticulate to oblique, obscure, leaves drying green, petals mostly 4–7 mm long, glabrous, ovary glabrous.

Distribution and ecology. This subspecies is confined to the Pacific drainage of Mexico and Central America from Sinaloa (Mexico) to Costa Rica. It is a tree of riversides, damp ravines and other wet places in tropical deciduous forest, and occasionally recorded from poorly drained savanna and mangrove. Generally at low altitude but ascending to 700 m in El Salvador and to 1000 m in Chiapas, Mexico, where it overlaps and intergrades with *Guarea glabra* subsp. *glabra*.

Representative additional collections. MEXICO. **Chiapas:** Escuintla, Acacoyagua (NW1592), *Matuda* 16639 (K). **Colima:** Manzanillo (NW19104), *Palmer* 1391 (G, GH, K, NY, US). **Guerrero:** Acapulco, rd. Puerto Marques (NW1699), *Miranda* 8407 (MEXU). **Jalisco:** Municipio la Huerta, Rio Cuitzmala (NW20105), *Lott* 703 (F, MEXU). **Nayarit:** Tres Marias Is. (NW21106), *Nelson* 4230 (A, F, GH, US). **Oaxaca:** Municipio San Miguel del Puerto, Dist. Pochutla, Xadani (NW1596), *Salas et al.* 2793 (NY). **Sinaloa:** Sierra Monterey, Quebrada de Platano, *H.S. Gentry* 5918 (NY).

GUATEMALA. **Escuintla:** near Rio Michatoya, SE of Escuintla (NW1592), *Standley* 89145 (F). **Santa Rosa:** region of Capulín, S of Los Cerritos (NW1490), *Standley* 79645 (F). **Zacatépequez:** Volcán de Fuego (NW1490), *J.D. Smith* 2601 (K).

EL SALVADOR. **Ahuachapán:** San Francisco Menendez, Montaña El Ojushtal (NW1389), *Castillo* s.n. (K). **La Libertad:** San Juan Opico Cerro el Jabali (NW1389), *Gonzalez & Hernandez* 368 (MO). **San Miguel:** Laguna de Aramuaca (NW1388), *Villacorta et al.* 2694 (K). **San Vicente:** vicinity of San Vicente (NW1388), *Standley* 21297 (NY).

NICARAGUA. **Carazo:** Rio Grande, 10 km from 'La Trinidad' (NW1186), *Araquistain* 3769 (K). **Chinandega:** Volcán Casita, Montañas El Uval (NW1287), *Grijalva A. & M.V.* 1459 (K). **Granada:** Volcán Mombacho, Laguna de Juan Tallo (NW1185), *Guzman et al.* 565 (K). **León:** Bellavista, Volcán Casita (NW1286), *Moreno* 24256 (K). **Managua:** road to Salamina, along Rio El Carmen (NW1186), *Stevens & Montiel* 17151 (K). **Rivas:** Bosque de Chococente, R. Escalante (NW1186), *Araquistain* 3795 (K).

COSTA RICA. **Guanacaste:** road Esparta to Cañas, junction to Juntas (NW0984), *Pennington* 10158 (NY). **Puntarenas:** Cantón de Aguirre, Savegre (NW0983), *Aguilar* 1190 (INB, K).

This subspecies is characterised by the usually oblanceolate leaflets with acute, obtuse or obtusely cuspidate apex, and the small \pm glabrous flowers. It is confined to damp places in tropical deciduous forest generally at low altitude, but material collected between 500 m and 1000 m grades imperceptibly with *Guarea glabra* subsp. *glabra*.

A population intermediate between *Guarea glabra* subsp. *excelsa* and *G. glabra* subsp. *glabrescens* occurs in the vicinity of Cuernavaca, Mexico at 1400–1500 m altitude. It has the axillary hair tufts and glabrous ovary of *Guarea glabra* subsp. *excelsa*, but the leaflet venation of *G. glabra* subsp. *glabrescens*. The specimens seen are *Pringle* 7074, *Bourgeau* 1197, *Croat & Hammon* 65773, *Hahn* s.n.

6c. *Guarea glabra* subsp. *microcarpa* (C.DC.) T.D.Penn., stat. nov. – *Guarea microcarpa* C.DC., Bull. Herb. Boissier, Sér. 2, 5: 420 (1905). – Type: Costa Rica, Cartago, Tucurrique, fl., fr., *Tonduz & Pittier* 13114 (holo G; iso BM, G, GH, K, M, US, W; photo NY). **Fig. 52B.**

?*Guarea brevianthera* C.DC., Smithsonian Misc. Collect. 68: 1 (1917). – Type: Costa Rica, La Palma, fl., *Tonduz* 12592 (holo US; iso NY (fragment)).

Guarea arcuata Coronado, Novon 16: 462 (2006), **syn. nov.** – Type: Costa Rica, Cartago, *Brown* 17521 (holo F).

Young shoots and inflorescences puberulous to glabrous, leaves glabrous (except for hair tufts), leaflets elliptic to broadly elliptic (often 2–3 times as long as broad), apex mostly acuminate, secondary veins 6–8 pairs, steeply ascending and strongly arcuate, tertiary veins numerous and close, oblique to perpendicular, leaves drying brownish, petals 5–8 mm long, glabrous, ovary glabrous.

Distribution and ecology. This subspecies is distributed from Nicaragua to Panama, and in South America from Ecuador to southern Peru. In Central America it occurs in wet montane forest between 700 m and 2200 m altitude. In South America it is present in both montane and lowland rain forest on the Pacific slopes and in lowland rain forest in Amazonian Ecuador and Peru.

Representative additional collections. NICARAGUA. **Boaco:** Cerro Mombachito, 5 km NW of Camoapa (NW1285), *Grijalva* 2853 (K). **Chontales:** Cerro Oluma, Cordillera Amerisque, *Gentry et al.* 43963 (K). **Jinotega:** Macizos de Peñas Blancas, vicinity of Finca of Manuel Estrada (NW1385), *Stevens* 11647 (K). **Matagalpa:** Cerro Matagalpa: Cerro Matapalo, 9 km from Matagalpa (NW1285), *Moreno & Robleto* 20468 (K).

COSTA RICA. **Alajuela:** Monteverde Biological Reserve, Rio Peñas Blancas (NW1084), *Haber & Bello* 7054 (CR, F, K, MO). **Cartago:** Turrialba, limite Sur del Monumento Nacional Guayabo (NW0983), *Rivera* 1946 (CR, F, K). **Guanacaste:** 3 km N of Santa Elena (NW1084), *Haber & Bello* 3810 (CR, K, MO). **Heredia:** Braulio Carillo National Park, Zurqui Station (NW1084), *Boyle* 2464 (CR, K). **Puntarenas:** Coto Brus, San Francisco de Sabalita (NW0882), *Alfaro* 4137 (INB); Cantón de Puntarenas, San Luis, Monteverde (NW1084), *Fuentes* 265 (K). **San José:** Acosta, Sabanillas (NW0984), *Sanchez et al.* 1152 (CR); NE of San Jeronimo, La Palma area (NW1084), *Burger & Visconti* 10212 (F).

PANAMA. **Bocas del Toro:** region of Cerro Colorado (NW0881), *McPherson* 8834 (K, MO). **Chiriqui:** Las Cumbres, NE of Cerro Punta (NW0882), *Schmalzel & Todzia* 2053 (K). **Cocle:** 7 km N of El Cope, Rivera Sawmill, *Folson et al.* 5687 (MO).

ECUADOR. **Carchi:** Gualpi Alto (NW0078), *Thomsen* 58825 (K, MO, NY, US). **Esmeraldas:** Awa Reserve, Mataje (NW0178), *Ortiz et al.* 37 (K, NY). **Guayas:** Canton Guayaquil, Bosque Protector Cerro Blanco (SW0279), *Rubio et al.* 1808 (MO). **Napo:** Aguarico, Reserva Etnica Huaorani (SW0076), *Aulestia M. & Gonti* 1976 (MO). **Pastaza:** Canton Pastaza, Pozo Petrolero ‘Moretecocha’ de ARCO (SW0177), *Gudiño et al.* 902 (MO, NY). **Pichincha:** Quito – Puerto Quito km 113, Rio Silanche Forest Reserve (NW0079), *Acevedo-Rodríguez et al.* 1706 (NY).

PERU. **Cuzco:** La Convención, below Echarate, Manguyari (SW1272), *Nuñez et al.* 10205 (MO). **Loreto:** Distrito Nauta, Rio Marañon, Caserio Florida (SW0473), *Rimachi* 4461 (NY). **Madre de Dios:** 39 km SW of Puerto Maldonado, Explorers Inn (SW1269), *Smith S.F. et al.* 962 (K, US).

This subspecies was treated as an informal 'race' of *Guarea glabra* in the *Flora Neotropica* treatment (Pennington *et al.*, 1981). It is defined by the generally broad leaflets c.2 times as long as broad, with few strongly arcuate and convergent secondary veins, and closely parallel, oblique or perpendicular tertiary venation. It is given formal subspecific rank here, due to the reasonable morphological distinctness allied to the ecology and geographical distribution in southern Central America and northwestern South America, which is commonly found in many other species. It is difficult to distinguish from *Guarea glabra* subsp. *glabra* in the West Indies, particularly Jamaica and the Leeward Islands.

6d. *Guarea glabra* subsp. *tuerckheimii* (C.DC.) T.D.Penn., stat. nov. – *Guarea tuerckheimii* C.DC. in Donn.Sm., Bot. Gaz. (Crawfordsville) 33: 250 (1902). – Type: Guatemala, Alta Verapaz, Cubilquitz, fl., von *Tuerckheim* 7835 (? holo G, not traced; iso GH, K, US). **Fig. 57D.**

?*Guarea kegelii* Turcz., Bull. Soc. Imp. Naturalistes Moscou 36: 589 (1863). – Type: Guatemala, fl., *Kegel* 12707 (holo LE, not traced).

Young shoots and inflorescences appressed puberulous to glabrous, leaves glabrous (except for hair tufts), leaflets elliptic to oblong-lanceolate, at least 3 times as long as broad, apex acuminate, secondary veins mostly 8–12 pairs, steeply ascending and arcuate, tertiary veins oblique, leaves drying brown, petals 5–7 mm long, usually with scattered appressed hairs, ovary glabrous.

Distribution and ecology. Distributed from Veracruz, Mexico to Costa Rica. It is a tree of wet lowland rain forest usually below 650 m altitude, but entering lower montane rain forest in Costa Rica (up to 1000 m altitude). Mostly confined to the Caribbean drainage, the only exception being in the Pacific drainage of Oaxaca and Chiapas (Mexico) and Guanacaste, Costa Rica.

Representative additional collections. MEXICO. **Chiapas:** Lacandona, Ríos Chancalah, Choc-oljahito and Tulija (NW1791), *Pennington & Sarukhán* 9174 (K, MEXU). **Oaxaca:** Distrito Miahuatlan, 17.9 km SW of San Jerónimo Coatlan (NW1696), *Torres & Campos* 10840 (F). **Puebla:** Municipio Ayotoxco, Ayotoxco (NW2097), *Ventura* 1000 (MEXU, MO). **Tabasco:** La Palma (NW1791), *Matuda* 3269 (K). **Veracruz:** Hidalgotitlan, Brecha Hnos. Cedillo – La Escuadra (NW1794), *Vásquez et al.* 43 (K).

GUATEMALA. **Alta Verapaz:** Municipio Panzos, 6 km SE of Telemán, Finca Mercedes (NW1589), *Stevens et al.* 25383 (K). **Huehuetenango:** between Ixtan and Río Ixtan, Sierra de los Cuatematanes (NW1591), *Steyermark* 49239 (F). **Izabal:** Santo Tomás del Castillo (NW1588), *Marshall et al.* 405 (NY). **Peten:** San Pedro, Cadenas road (NW1589), *Contreras* 9490 (NY).

BELIZE. **Cayo:** 4 miles S of Grand de Oro, *Dwyer* 10914 (MO). **Stann Creek:** Middlesex (NW1688), *Gentle* 2899 (F, K, NY). **Toledo:** Maya Mountains Bladen Nature Reserve (NW1688), *Holst et al.* 5364 (K).

HONDURAS. **Atlántida:** 5 km SW of La Ceiba, Danto River (NW1586), *Hazlett* 3236 (F, K). **Comayagua:** Lake Yojoa, Pito Solo (NW1487), *Edwards* 410 (K). **Cortes:** Lake Yojoa, between Las Flores and Balincito (NW1487), *Nelson et al.* 5885 (K). **Gracias a Dios:** R. Patuca, Krautara (NW1584), *Pennington et al.* 13676 (K, MO). **Olancho:** Río Olancho, between

San Esteban and Bonito Oriental (NW1585), *Croat & Hannon* 64414 (MO). **Yoro**: Cascada de Rio Guan Guan (NW1587), *Hawkins & Merello* 776 (K).

COSTA RICA. Guanacaste: Parque Rincón de la Vieja, Hacienda Santa Maria (NW1085), *Herrera* 919 (K). **Puntarenas**: Cantón de Coto Brus, Cordillera de Talamanca, Rio Coton (NW0882), *Moraga* 292 (K).

Closest to *Guarea glabra* subsp. *glabra* but distinguished by the slightly longer leaflets (15–)20–25 cm long, with a long acuminate apex, 8–12 steeply ascending and arcuate secondary veins, and the often rather long inflorescence (15–25 cm long). The corolla size and glabrous ovary are as in *Guarea glabra* subsp. *glabra*. Dried specimens often look distinct on account of drying brown, whereas the other subspecies tend to dry green.

The identity of *Guarea kegelii* is still uncertain, as the type collection has not been traced. It clearly belongs in *Guarea glabra*, because the leaflets are described as being glabrous except for having hair tufts in the vein axils on the lower surface. It could belong in either *Guarea glabra* subsp. *tuerckheimii* or in *G. glabra* subsp. *glabra*, both of which have leaves which are glabrous except for axillary hair tufts. The name *Guarea kegelii* has recently been misapplied to *G. bijuga* (Coronado, 2006; Rodríguez, 2006), a species lacking hair tufts in the vein axils.

6e. *Guarea glabra* subsp. *glabrescens* (Hook. & Arn.) T.D.Penn., **stat. nov.** – *Sapindus glabrescens* Hook. & Arn., Bot. Beechey Voyage 281 (1838). – *Guarea glabrescens* (Hook. & Arn.) Blake, Contr. U.S. Natl. Herb. 23: 559 (1923). – Type: Mexico (probably Tepic [NW21104]), fr., *Beechey* s.n. (holo K). **Fig. 58A.**

Guarea fulva Triana & Planch. var. *mexicana* C.DC. in A.DC. & C.DC., Monogr. Phan. 1: 575 (1878). – Type: Mexico, Tepic, fr., *Beechey* s.n. (holo K).

Young shoots and inflorescences pubescent to tomentose, leaflets pubescent on midrib and veins below, leaflets elliptic to oblong-elliptic, apex shortly acuminate, secondary veins 12–16 pairs, ascending, slightly arcuate, tertiaries oblique to reticulate, leaves drying green to brown, petals 4–5 mm long, appressed pubescent, ovary pubescent.

Distribution and ecology. Known only from a few collections in the states of Mexico, Guerrero, Jalisco and Nayarit, where it inhabits shady ravines in ‘selva mediana caducifolia’, between 400 m and 1300 m altitude.

Collections examined. MEXICO. **Guerrero**: Teloapán, rd. Iguala to Ciudad Altamirano (NW1899), *Martinez* 622 (MEXU); Mina (NW18100), *Hinton et al.* 10097 (K, MO, NY); Distrito Adama, Ahotla (NW18100), *Mexia* 8900 (K), *Reko* 4896 (K). **Jalisco**: Municipio Tecalitlan, before Alotitlan (NW19103), *Machuca & Chazaro* 6638 (MEXU); Municipio Cuhautitlan, 6 km from Telcruz (NW19104), *Ramirez et al.* 228 (MEXU). **Mexico**: 25 km S of Amatepec, Terraceria Amatepec-Arcelia (NW18100), *Flores & Terpan* 748 (MEXU); District Temascaltepec, Vigas (NW19100), *Hinton* 3818 (K, NY); District Temascaltepec, Acatitlán (NW19100), *Hinton et al.* 6189 (K); District Temascaltepec, Nanchititla (NW19100), *Hinton et al.* 7542 (K, NY, US); District Temascaltepec, Luvianos (NW19100), *Hinton et al.* 7553

(K, NY, US). **Michoacán:** Municipio la Huacana, 7 km W of Los Ranchos (NW18102), *Steinmann* 4362 (MEXU). **Nayarit:** Municipio Compostela la Cascada, 9 km NW of Mesillas (NW21105), *Flores et al.* 901 (MO).

This subspecies is closest to *Guarea glabra* subsp. *excelsa* and shares part of its range. It differs in its pubescent leaflets and more numerous secondary veins and in the pubescent ovary. In other respects of floral size and structure it is identical. An intermediate population occurs in the vicinity of Cuernavaca, Morelos (specimens seen are *Hahn* s.n., *Croat & Hannon* 65773, *Bourgeau* 1197 and *Pringle* 7074). This population shares the same leaflet size and shape as *Guarea glabra* subsp. *glabrescens*, but lacks the leaflet indumentum, apart from hair tufts in the vein axils, and has a glabrous ovary.

6f. *Guarea glabra* subsp. *rovirosae* (C.DC.) T.D.Penn., stat. nov. – *Guarea rovirosae* C.DC., *Annuaire Conserv. Jard. Bot. Genève* 10: 145 (1907). – Type: Mexico, Tabasco, near Atasta, fl., *Rovirosa* 542 (holo US; iso K, NY, PH). **Fig. 58B.** *Guarea petenensis* Coronado, *Novon* 16: 463 (2006), **syn. nov.** – Type: Guatemala, Petén, Rio Pasión, Rio Pucte tributary below Sayaxche, between Pucte and La Libertad, fl., *Lundell* 18164 (holo MO).

Young shoots and inflorescences stiffly pubescent with pale hairs, leaflets usually with some pubescence on midrib and veins below, leaflets elliptic, apex acuminate, secondary veins 7–11 pairs, ascending, arcuate, tertiary veins reticulate to oblique, leaves drying green, petals mostly 4.5–6.5 mm long, usually with scattered appressed hairs, ovary sparsely strigose or glabrous.

Distribution and ecology. Atlantic and Pacific drainage of southern Mexico, from Oaxaca, Puebla and Veracruz to southern Yucatan Peninsula, Belize and Honduras. It is a small tree of lowland evergreen rain forest, mostly below 500 m altitude, but present in montane rain forest at 1350 m altitude in the region of Los Tuxtlas, Veracruz, Mexico.

Representative additional collections. MEXICO. **Chiapas:** Municipio Ocosingo, Yaxchilan (NW1690), *Gutierrez* 911 (MO). **Oaxaca:** Municipio Sta. Maria Chimalapa, Rio Verde (NW1694), *Caletti et al.* 123 (MO). **Puebla:** Rancho El Ajenjibre, *Pennington & Sarukhán* 9294 (K, NY). **Tabasco:** Balancán, Achotal (NW1791), *Matuda* 3085 (F). **Veracruz:** Volcán San Martín (NW1895), *Nevling & Gomez-Pompa* 2530 (K).

GUATEMALA. **Izabal:** Santo Tomas de Castilla, road to Las Pavas (NW1588), *Marshall et al.* 418 (NY). **Petén:** Santa Elena, Laguna Turicentro (NW1689), *Ortiz* 938 (F).

BELIZE. **Cayo:** Chiquibal Forest Reserve, 1 km from Las Cuevas (NW1688), *Ibañez* A69 (MO). **Orange Walk:** Indian Church (NW1788), *Arnason & Lambert* 17033 (MO). **Toledo:** Punta Gorda, Sand Hill (NW1688), *Schipp* 1001 (K).

HONDURAS. **Comayagua:** 7 km N of La Libertad (NW1487), *Hazlett* 1688 (MO). **Olancho:** Valle de Catacamas, near Santa Maria del Real (NW1485), *Molina* 8423 (F). **Yoro:** road to Yorito (NW1587), *Hazlett* 3240 (K).

This subspecies was not given formal rank in the *Flora Neotropica* treatment (Pennington *et al.*, 1981), but was included within the informal ‘race *glabra*’.

However, in a recent multivariate analysis of the *Guarea glabra* complex (Coronado, 2003) it was recognised as a distinct species, *G. petenensis*. It is characterised by the elliptic leaflets with an acuminate apex, the rather stiff pale indumentum on the young parts, also usually present at least on the midrib and veins of the lower leaflet surface, and by the presence of sparse appressed pubescence on the petals and ovary. The leaves usually dry pale green. On the basis of its restricted distribution and the partial morphological distinctness (there are many intermediates with *Guarea glabra* subsp. *tuerckheimii*), we are recognising it at subspecific level with the earlier epithet *rovirosae*.

7. *Guarea tonduzii* C.DC., Smithsonian Misc. Collect. 68(6): 4 (1917). – Type: Costa Rica, near San Ramon, Tremedal, fr., *Tonduz* 17677 (holo G; iso BM, CR, F, G, M, S, US, W). **Fig. 58C.**

Guarea glabra auct. non Vahl: T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 269 (1981), p.p.

Guarea adenophylla Al.Rodr., Lankesteriana 6: 102 (2006), **syn. nov.** – Type: Costa Rica, Puntarenas, Monteverde, Pacific slope, Campbell Farm, fl., *Haber & Zukowski* 10791 (holo INB; iso CR, K).

Young shoots 3–5 mm diam., tomentose (golden hairs) at first, soon glabrous and becoming pale whitish grey with some raised brown lenticels. *Leaves* pinnate with an active terminal bud, petiole 2.5–6 cm long, semiterete to terete, tomentose at first, becoming glabrous, rhachis up to 40 cm long, terete, pubescent at first, soon becoming glabrous and eventually woody; petiolule 3–8 mm long, tomentose at first, becoming glabrous. *Leaflets* opposite, up to 7 pairs, (11–)13–20(–22.5) × (5–)5.1–7(–9.8) cm, broadly elliptic to broadly oblanceolate, apex acuminate or rarely obtusely cuspidate, base acute, narrowly cuneate or obtuse, coriaceous, upper surface pubescent along the midrib or glabrous, lower surface tomentose to pubescent along the midrib and secondary veins, becoming glabrous on the lamina, sparse to dense minute red papillae nearly always present, occasionally glandular-punctate or -striate; axillary hair tufts absent, venation eucamptodromous, midrib flat on the upper surface, secondaries 9–13(–14) pairs, moderately to steeply ascending, slightly arcuate, slightly convergent, intersecondaries usually absent, tertiaries oblique, rather widely spaced, coarse higher order reticulum visible below. *Inflorescence* axillary or on twigs below the leaves, 3–10 cm long, a panicle with the lower lateral branches to 5 cm long, ultimate branches sometimes cymose, tomentose to coarsely pubescent; pedicel 2–3 mm long (above the articulation), tomentose to pubescent. *Calyx* 1.5–3(–4) mm long, patelliform to shortly cup-shaped, shallowly to moderately 4-lobed or -toothed, pubescent to subglabrous outside, glabrous inside. *Petals* 4(–5), male and female 8–12 × 2–3 mm, strap-shaped, apex acute, densely pubescent to subglabrous with a few appressed hairs outside, glabrous inside. *Staminal tube* 7–10 × 2–3 mm, tubular (male) to ellipsoid (female), margin truncate to obscurely lobed, glabrous; anthers 8(–10), 8–13 mm long, ellipsoid, glabrous, antherodes in female

shrunken, without pollen. *Nectary* 1–1.5 mm long, a stipe usually expanded into a broad collar beneath the ovary, glabrous. *Ovary* 1.5–2 mm long, ovoid, 4-locular, locules 1-ovulate, usually densely pubescent, rarely only sparsely pubescent, male with rudimentary ovules, style 1.5–2 mm long, glabrous, style-head discoid. *Capsule* 1.5–2.8 × 1.5–2.8 cm, globose, apex and base rounded, 4-valved, pericarp 1.5–3 mm thick, rough and rather scurfy, sparsely to densely pubescent at first, usually maturing glabrous. *Seeds* usually 3–4, 1.3–2.4 cm long, shaped like the segment of an orange; embryo with thick plano-convex, superposed to oblique cotyledons, radicle abaxial, included or extending to the surface.

Field characters. Tree to 25 m high and 50 cm diam., often flowering when less than 5 m high. Bark greyish brown, smooth or scaling in small thin pieces, slash pink, with the characteristic scent of the family. Flowers with greenish-cream or pale green petals and whitish staminal tube; mature fruit red, orange or brown; the seed surrounded by an orange sarcotesta. Flowering in Costa Rica is recorded from November to April, with mature fruit throughout the year. In Panama it is from February to March, with a single record of mature fruit in March.

Distribution and ecology. The species occurs only in Costa Rica and Panama, where it is a component of montane rain forest mostly between 700 m and 1800 m altitude, rarely up to 2200 m. Specimens from Honduras and Mexico previously referred to this species belong in *Guarea bullata*.

Representative additional collections. COSTA RICA. **Alajuela:** Zarcero (NW1084), *A. Smith* 4108 (F). **Guanacaste:** Monteverde (NW1084), *Gentry et al.* 71564 (MO). **Heredia:** Vara Blanca de Sarapiquí (NW1084), *Skutch* 3621 (US). **Puntarenas:** Monteverde, Pacific Slope, Campbell Farm (NW1084), *Haber & Zukowski* 10791 (CR, INB, K). **San José:** Dota, Santa Maria de Dota (NW0983), *Hammel et al.* 24065 (INB).

PANAMA. **Bocas del Toro:** Chiriqui border, Fortuna Dam area (NW0882), *McPherson* 8627 (MO). **Chiriqui:** between Gualaca and Fortuna Dam site (NW0882), *Croat* 49955 (MO). **Veraguas:** Cordillera de Tute, just W of Santa Fé (NW0881), *Knapp & Cress* 4339 (K).

Guarea tonduzii is morphologically close to *G. bullata*, a relationship which is confirmed by the ITS phylogeny, and although the latter is mostly found in lowland forest, both species occur together in montane forest in Costa Rica. The stiff erect or spreading indumentum of *Guarea bullata* is generally distinct from the more tomentose indumentum of *G. tonduzii*, and the primary, secondary and tertiary venation of *G. bullata* is nearly always impressed (often strongly so) on the upper surface, whereas that of *G. tonduzii* is not. The flowers are of similar size, but the ovary of *Guarea bullata* is usually sparsely strigose, whereas that of *G. tonduzii* is densely pubescent. The fruit of *Guarea bullata* is smooth whereas that of *G. tonduzii* is generally rough-skinned and scurfy. On this basis a few specimens from Mexico and Honduras which were formally regarded as belonging to *Guarea tonduzii* are here placed in *G. bullata*.

Vegetative specimens of *Guarea tonduzii* can also be confused with *G. glabra* subsp. *microcarpa* where the two occur together in montane forest in Costa Rica, but

the leaflets of *G. tonduzii* are generally more coriaceous with more numerous secondary veins and they lack the fine parallel tertiary venation which is characteristic of *G. glabra* subsp. *microcarpa*.

The recently described *Guarea adenophylla*, distinguished on the basis of the numerous minute red papillae on the leaf undersurface, is here reduced to synonymy. The presence of minute red papillae is widespread in the genus and in *Guarea tonduzii* their presence varies from abundant to sparse and provides no basis for subdivision. The leaf indumentum of this species provides a similar example, varying from dense to almost glabrous. The phylogenetic analysis confirms the close relationship of *Guarea tonduzii*, *G. chiricana* and *G. bullata*.

8. *Guarea chiricana* Standl., [Trop. Woods 16: 18 (1928), nom. nud.] Publ. Field Mus. Nat. Hist., Bot. Ser. 4(1): 215 (1929). – Type: Panama, Chiriqui, Progreso, fl., *Cooper & Slater* 164 (lecto F, designated by Pennington in Pennington *et al.* (1981: 269); isolecto NY, US, Y). **Fig. 58D.**

Guarea glabra auct. non Vahl: T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 269 (1981), p.p.

Guarea pilosa Al.Rodr., Lankesteriana 6: 113 (2006), **syn. nov.** – Type: Costa Rica, Alajuela, Rincon de la Vieja National Park, Rio Jala Piedras, N slope of Volcán Santa Maria, fr., *G. Rivera* 1098 (holo INB; iso CR, K).

Young shoots 3–5 mm diam., pubescent at first with stiff erect and spreading pale hairs, usually becoming glabrous, smooth, whitish grey with a few lenticels. *Leaves* pinnate with an active terminal bud, petiole 2.5–5 cm long, semiterete, stiffly pubescent to glabrous, rhachis eventually up to 55 cm long, slightly channelled on the upper surface, stiffly pubescent to glabrous; petiolule 3–5 mm long, pubescent at first, soon glabrous. *Leaflets* opposite, 2–4(–5) pairs, (12–)16–25(–31) × (4.6–)5.5–9.5(–17) cm, elliptic, apex acuminate, base acute, chartaceous, upper surface glabrous except for the sometimes stiffly pubescent midrib, lower surface stiffly pubescent on midrib and veins or glabrous, drying pale green on both surfaces, not glandular-punctate or -striate; venation eucamptodromous, midrib slightly sunken on the upper surface, secondaries (9–)10–15(–16) pairs, ascending, straight or slightly arcuate, parallel or slightly convergent, flat or sunken on the upper surface, (rarely strongly sunken and leaves bullate), intersecondaries few or absent, tertiaries oblique, parallel; higher order venation finely reticulate and visible on both surfaces. *In-florescence* axillary or on twigs below leaves, 4–15 cm long, often branched near the base and with several slender paniculate branches, indumentum of stiff erect and spreading pale hairs, sometimes becoming glabrous with age, ultimate branchlets and solitary flowers subtended by a minute bract bearing a tuft of stiff pale hairs; pedicel 1.5–2 mm long (above the articulation), glabrous. *Flowers* unisexual (plant dioecious). *Calyx* 1–1.5 mm long, patelliform, with 4 small teeth or lobes, or ± truncate, with a few scattered hairs outside or glabrous. *Petals* 4, male 8–10 × 1–1.5 mm, female 6.5–8 × 1–1.5 mm, strap-shaped, apex acute, free, valvate, usually glabrous or rarely

with sparse short appressed indumentum. *Staminal tube* in male 6–8 × 1.5–2 mm, female 6–6.5 × 1.5 mm, tubular, margin entire or slightly irregular, glabrous; anthers 8, 0.6–0.7 mm long, oblong, glabrous, antherodes in female similar but not dehiscent. *Nectary* 1–1.5 mm long, expanded into a collar below the ovary, glabrous, slightly shorter and with a less obvious collar in the female. *Ovary* 1–2 mm long, ovoid, 4-locular, locules 1-ovulate, usually with sparse stiff pale indumentum, rarely densely strigose or glabrous, male with rudimentary ovules, style 1.5–3 mm long, glabrous, style-head discoid. *Capsule* 1.3–2 × 1.6–2 cm, obovoid to globose, apex rounded or truncate, base obtuse, sometimes with a short stipe, 4-valved, pericarp 1–1.5 mm thick, fleshy, smooth, glabrous or occasionally with scattered residual pubescence, lenticellate or not. *Seeds* 2–4, 1–1.6 cm long, shaped like the segment of an orange; embryo with thick plano-convex, superposed cotyledons, radicle abaxial, extending to the surface.

Field characters. Treelet or small tree to 25 m high and 35 cm diam., but flowering as a small treelet 1–3 m high. Trunk of larger specimens fluted at the base and with pale buff-coloured bark scaling in small deep irregular pieces, slash pale cream, 6–7 mm thick, with characteristic spicy Meliaceous scent. The flowers are whitish and the fruit matures red or pink. The seed is surrounded by a bright orange sarcotesta, which contrasts with the white inner surface of the pericarp. Flowering throughout the range is from December to June. Mature fruit are recorded in February (Nicaragua), January and April to September in Costa Rica, and January, March and October to December in Panama.

Distribution and ecology. Nicaragua, Costa Rica, Panama and Colombia in primary and old secondary lowland and montane rain forest from sea level to 1200(–1500) m altitude. It occurs on both the Atlantic and Pacific drainages in Costa Rica.

Representative additional collections. NICARAGUA. **Rio San Juan:** 1 km E of Rio Sabalos (NW1184), *Moreno* 23184 (K, MO). **Zelaya:** Municipio Nueva Guinea, Boca de Piedra (NW1184), *Laguna* 129 (K).

COSTA RICA. **Alajuela:** Monteverde Biological Reserve, Rio Peñas Blancas (NW1084), *Haber & Cruz* 7102 (CR, MO). **Guanacaste:** Liberia, PN Guanacaste, Cacao (NW1085), *Soto & Rojas* 1751 (INB). **Heredia:** La Selva Biological Station, Rio Sarapiquí and Rio Puerto Viejo (NW1084), *Grayum & Longino* 9307 (CR, K, MO). **Puntarenas:** Rincón de Osa, between Rincón & Playa Blanca (NW0883), *J. & K. Utley* 1246 (MO); P.N. Isla del Coco, Bahía Chattan (NW0587), *Quesada* 1121 (K). **San José:** Dota, track to Tijerilla (NW0983), *Valverde* 838 (F, K); Acosta, Cuenca del Pirris-Damas (NW0984), *Morales* 8145 (INB).

PANAMA. **Bocas del Toro:** near highway to Chiriqui Grande (NW0882), *McPherson* 11814 (MO). **Canal Zone:** 12 miles S of Colon, vicinity La Providencia (NW0979), *Blum & Tyson* 2335 (MO). **Chiriquí:** Puerto Armuelles to San Bartolo Limite (NW0882), *Croat* 35061 (K, MO). **Cocle:** 7 km N of El Cope, Alto Cavario (NW0880), *Folsom* 4169 (K, MO). **Colon:** Salud (NW0980), *Lao & Holdridge* 174 (MO). **Panama:** Parque Nacional Altos de Campana (NW0879), *Galdames* 1075 (F). **San Blas:** El Llano–Carti road, 19.1 km from Interamerican Highway (NW0978), *de Nevers* 3778 (K). **Veraguas:** Cerro Tute, Cordillera de Tute, W of Santa Fe (NW0881), *Knapp & Sytsma* 2580 (K).

COLOMBIA. **Antioquia:** Municipio Taraza, Corregimiento ‘El 12’ (NW0775), *Callejas & Betancur* 3518 (K, NY).

Guarea chiricana differs from *G. glabra* in lacking the hair tufts in the axils of the secondary veins and in the distinctive indumentum of the young shoots, lower leaf surface and inflorescence. It also has slightly more numerous secondary veins, and the higher order venation forms a fine reticulum which is visible on both surfaces. Its corolla is generally slightly longer than that of *Guarea glabra* and the ovary generally has some indumentum. It differs from *Guarea bijuga* in the characteristic indumentum of the young shoots, leaves and inflorescence, shorter calyx, pubescence of the ovary and smooth capsule. The finely reticulate higher order venation also distinguishes it from *Guarea bullata*, and its leaflets are rarely bullate and they dry pale green on both surfaces (brown in *G. bullata*). The corolla of *Guarea chiricana* is nearly always glabrous whereas that of *G. bullata* has stiff dense appressed pubescence.

Guarea chiricana is most likely to be confused with *G. glabra* subsp. *rovirosae* which has a similar venation and leaflet shape. It differs in the more numerous secondary veins, and in the longer and more slender, usually glabrous corolla.

Guarea pilosa is here reduced to synonymy. It is a slightly more pubescent form of the species and distributed throughout its range.

A small number of collections from the Fortuna Dam area, Chiriqui, Panama, are included in this species with some reservations. They differ from typical *Guarea chiricana* in their slightly to strongly bullate leaflets. The fruit are typical of the species, but the flowers have not yet been collected. The collections seen are *Churchill et al.* 4765 (MO), *Galdames et al.* 647 (K), *McPherson* 7698 (K), *Valdespino et al.* 470 (NY) and *Valdespino et al.* 583 (MO).

9. *Guarea bullata* Radlk., Bull. Herb. Boissier, Sér. 2, 5: 192 (1905). – Type: Costa Rica, Cartago, Tucurrique, fr., *Tonduz* 12838 (holo CR; iso BM, M, P). **Figs 8, 59A.** *Guarea glabra* auct. non Vahl: T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 269 (1981), p.p.

Young shoots 3–6 mm diam., densely pubescent with pale straw-coloured to ferruginous stiff erect or spreading hairs, eventually becoming glabrous, pale greyish white, smooth, with some elongate lenticels. *Leaves* pinnate with an active terminal bud, petiole 2.5–5 cm long, semiterete, pubescent, eventually becoming glabrous, rhachis to 50 cm long, semiterete and sometimes channelled on the upper surface, pubescent at first with stiff, erect or spreading hairs, becoming glabrous and woody as the lower leaflets fall; petiolule 3–6(–10) mm long, pubescent. *Leaflets* opposite, up to 8 pairs, (9.2–)12–20(–31) × (2.7–)4.2–6(–7.4) cm, elliptic to oblanceolate, apex nearly always acuminate, rarely obtusely cuspidate, base acute to narrowly cuneate, thinly coriaceous, upper surface glabrous except for residual indumentum along the midrib, lower surface with stiff erect or spreading pubescence along the midrib and secondary veins, becoming glabrous with age, drying brown, sparsely glandular-striate; venation eucamptodromous, midrib sunken on the upper surface, secondaries (10–)11–15(–16) pairs, moderately to steeply ascending, straight or slightly arcuate, parallel or slightly convergent, intersecondaries moderately



FIG. 8. *Guarea bullata* Radlk. A, young leaf; B, habit; C, dormant bud at leaf apex; D, flower bud; E, half-flower; F, fruit. (A, D-E, Herrera 918; B, C, Skutch 2665; F, Liesner 2039).

developed or absent, tertiaries oblique, parallel, secondary and tertiary venation often strongly impressed on the upper surface (bullate). *Inflorescence* axillary or on old wood below the leaves, 3–10 cm long, often clustered, a slender or narrowly pyramidal thyrse, the lower branches up to 3 cm long, sparsely to densely pubescent with stiff erect or spreading hairs; pedicel 1–3 mm long, pubescent. *Calyx* (1–)2–3 mm long, patelliform to cup-shaped, margin entire or with 4 shallow teeth or lobes, with sparse stiff pubescence outside, glabrous inside. *Petals* 4, (male and female) 7–11 × 1.5–3 mm, strap-shaped, apex acute, free, valvate, with pale stiff appressed pubescence outside, glabrous inside. *Staminal tube* (male and female) 5–9.5 × 2–3 mm, tubular, margin undulate, glabrous; anthers 8(–10), 1–1.2 mm long, oblong, glabrous, antherodes in female similar but not dehiscent. *Nectary* 1.5–2.5 mm long, a stipe expanded into a broad collar below the ovary, shorter, broader and less expanded in the female. *Ovary* c.2 mm long, 4(–5)-locular, locules 1-ovulate, ovoid, nearly always sparsely strigose, rarely glabrous, male more slender with rudimentary ovules, style 1.5–3.5 mm long, glabrous, style-head discoid. *Capsule* 1.5–3.2 × 1.5–3.5 cm, globose or turbinate, apex rounded to truncate, base rounded or obtuse, 4(–5)-valved, valves 1-seeded, pericarp 2–5 mm thick, smooth, nearly always glabrous (densely pubescent in Honduras), often lenticellate. *Seeds* 3–5, 1.2–2.5 cm long, shaped like the segment of an orange; embryo with thick plano-convex, obliquely superposed cotyledons, radicle abaxial, extending to the surface.

Field characters. Tree to 20(–35) m high and 80 cm diam., but often flowering as a small treelet of 3–10 m high; bark brown, shallowly fissured and slash with the characteristic Meliaceous scent; flowers creamish-white or rarely tinged with pink; the fruit maturing pink, red or orange. Flowering in Mexico is recorded in June and August, but in Costa Rica throughout the year, and records of mature fruit vary widely: July (Mexico), May (Honduras), mostly January to August (Costa Rica), February to March (Panama), October to November (Colombia) and August (Ecuador).

Distribution and ecology. Distributed southwards from the Caribbean slopes of Veracruz, Mexico to Chiapas and along the Caribbean drainage of Honduras and Nicaragua to Costa Rica, Panama, Colombia and Pacific Ecuador. Not yet recorded from Belize or El Salvador. A species of lowland and montane rain forest from near sea level to 1200 m altitude.

Representative additional collections. MEXICO. **Oaxaca:** Municipio Santa Maria, Chimalapa, 10 km S of Santa Maria (SW1694), *Hernandez* 1401 (MO). **Veracruz:** San Andrés Tuxtla, Los Tuxtlas Tropical Biological Station (NW1895), *Ibarra & Sinaca* 1757 (MO, NY).

HONDURAS. **Atlántida:** N slope of Pico Bonito, E of new CURLA (NW1585), *Evans* 1581 (K).

NICARAGUA. **Rio San Juan:** Bocas de Sabalo (NW1184), *Moreno* 26755 (MO). **Zelaya:** El Achote (NW1184), *Araquistain* 3135 (K).

COSTA RICA. **Alajuela:** Canton de San Carlos, 1.5 km S of Chachagua (NW1084), *Haber* 11797 (INB, K); Upala, Cuenca del Zapote, El Pilon (NW1085), *Jiménez & Lopez* 181 (INB). **Cartago:** Turrialba, Potrero Rejoyon (NW0983), *Pennington & Budowski* 10108 (NY).

Guanacaste: Parque Rincón de la Vieja (NW1085), *Herrera* 918 (CR, F). **Heredia:** Finca la Selva, OTS Field Station (NW1084), *Chacón* 1122 (MO). **Limón:** Talamanca, Finca la Culebra (NW0982), *Gomez-Laurito & Gomez* 12342 (CR). **Puntarenas:** Golfo Dulce Forest Reserve, Aguabuena (NW0883), *Aguilar* 708 (INB, K). **San José:** vicinity of El General (NW0983), *Skutch* 2665 (K, NY, US).

PANAMA. **Bocas del Toro:** Quebrada Bonyic (NW0982), *Santamaria & Lara* 1098 (MO). **Darien:** Distrito Pinogama, Corregimiento El Real, 6 km E of El Real (NW0877), *Berry et al.* 5421 (K). **Antioquia:** Municipio Turbo, road Tapon del Darien km 11 (NW0876), *Brand & Gonzalez* 509 (MO).

ECUADOR. **Esmeraldas:** Anchayacu, Eloy Alfaro, Mayronga (NW0079), *Pennington et al.* 14928 (NY). **Los Ríos or Pichincha:** Patricia Pilar to 24 de Mayo, El Centinela (SW0079), *Dodson & Gentry* 12420 (F, MO).

COLOMBIA. **Antioquia:** Municipio Mutatá, Río Surumbay (NW0776), *Callejas et al.* 5747 (K, MO).

This species differs from *Guarea glabra* in lacking the hair tufts in the vein axils, in the stiff spreading or erect indumentum on the young shoots, lower leaf surface and inflorescence, in the impressed venation on the upper leaflet surface (often bullate), and in its longer petals with appressed indumentum, and in the usually sparsely strigose ovary. It is sometimes difficult to distinguish from *Guarea tonduzii* where the two species co-occur in montane rain forest in Costa Rica, as both have a similar indumentum and flower size.

10. *Guarea kunthiana* A.Juss., Bull. Sci. Nat. Géol. 23: 240 (1830); Mém. Mus. Hist. Nat. 19: 241, 290 (1831); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 312 (1981). – Type: French Guiana (Cayenne), fl., fr., *Poiteau* s.n. (holo P-JU (without data); iso G, K). **Figs 9, 63A.**

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 312–313 (1981).

Abbreviated description. Young shoots and inflorescences appressed puberulous to sparsely or densely softly pubescent, leaves with a terminal bud showing intermittent growth, leaflets 2–6(–10) pairs (leaves rarely 1-foliolate), (10–)15–25(–34) × (3.5–)5–10(–20) cm, elliptic or oblanceolate, chartaceous to coriaceous, usually glabrous, less frequently lower surface sparsely to densely puberulous or softly pubescent, higher order (tertiary) venation obscure, inflorescence usually axillary, often with indeterminate apical growth (1–)3.5–25(–30) cm long, a pyramidal thyrses, lower branches to 12 cm long, petals (3–)4, valvate, (6–)7–12(–13.5) mm long, staminal tube 5.5–10 mm long, (1.5–)2–3(–4) mm broad, often narrowed at the apex, anthers (7–)8(–10), ovary (3–)4-locular, locules with 2 superposed ovules, nearly always glabrous, capsule 1.5–4.5(–7.5) × 1.5–3.5(–6.5) cm, ellipsoid to globose, usually somewhat constricted between the seeds, and often slightly quadrangular in section, smooth, glabrous, usually with pale lenticels, 4-valved, pericarp 1–4 mm thick, valves with 2 superposed seeds.

Distribution and ecology. From Nicaragua southwards across the whole of tropical South America to Bolivia, Paraguay, southern Brazil and northern Argentina. Also

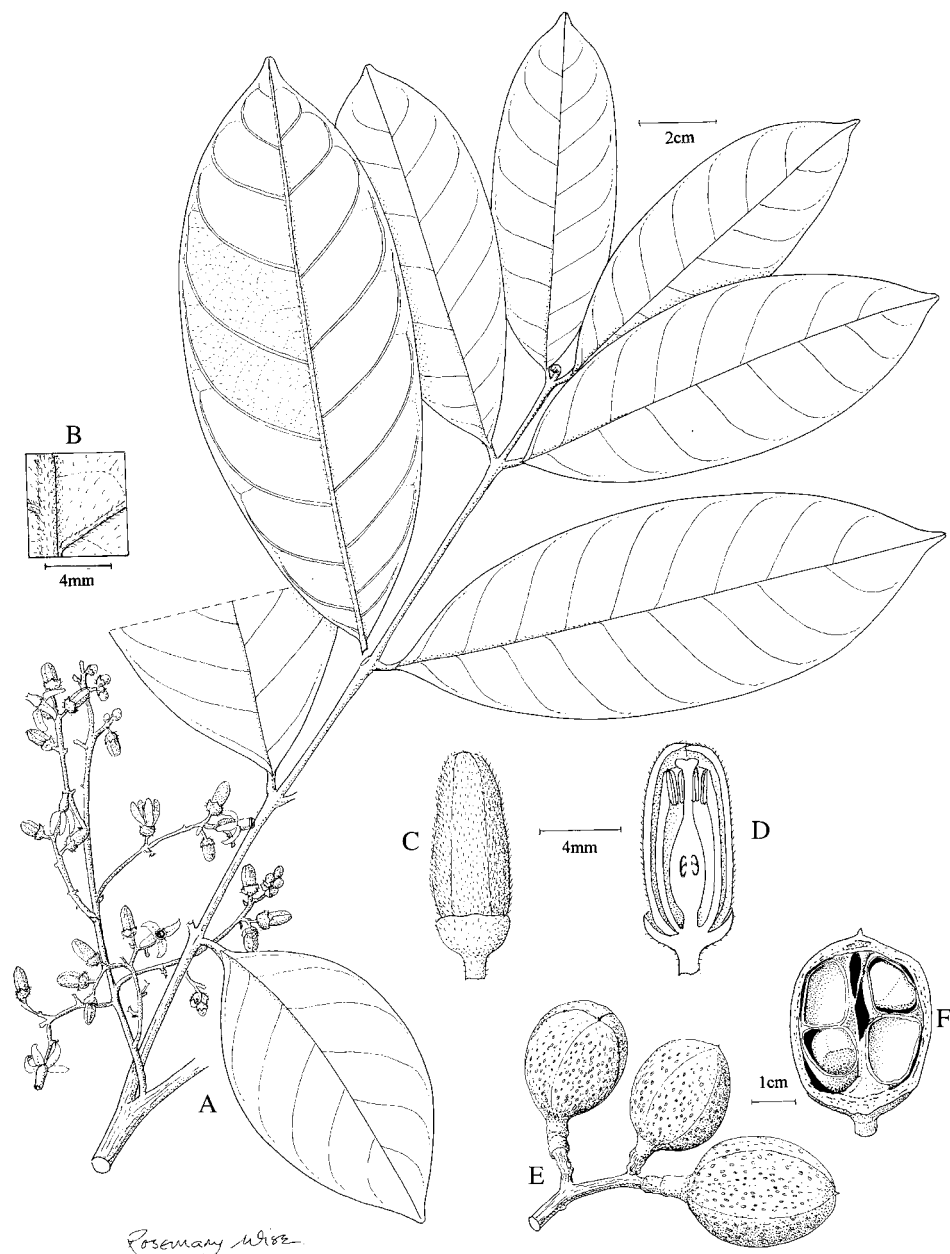


FIG. 9. *Guarea kunthiana* A.Juss. A, habit; B, enlargement of leaf undersurface; C, flower bud; D, half-flower; E, fruit; F, section of fruit. (A, B, Wallnöfer & Tarin 13497; C, D, Mori & Pipoly 15615; E, Mori & Gracie 18330; F, Jaramillo *et al.* 656).

present in the Lesser Antilles (Dominica and Martinique). A common component of evergreen lowland rain forest on non-flooded land and also ascending to wet montane forest in the Andes (up to 2500 m altitude). In the drier, more seasonal areas of southeastern Brazil it is confined to gallery forest along rivers.

Representative additional collections. NICARAGUA. **Rivas:** Isla Ometepe, Volcan Maderas (NW1185), *Robleto* 741 (K).

COSTA RICA. **Alajuela:** Upala, Colonia Libertad (NW1085), *Herrera* 1964 (K). **Cartago:** Rio Grande de Orosi, Tapanti (NW0983), *Grayum & Sleeper* 3452 (MO). **Guanacaste:** 3 km N of Santa Elena (NW1084), *Haber ex Bello* 3799 (K). **Limón:** Cerro Coronel (NW1083), *Stevens* 23849 (K). **Puntarenas:** Cantón Golfito, PN Corcovado, Sirena (NW0883), *Aguilar* 3437 (INB); Nicoya Peninsula, Curu (NW0984), *Sanders et al.* 19289 (MO).

PANAMA. **Chiriquí:** Fortuna Dam region, Quebrada Arena (NW0882), *McPherson* 8729 (K).

WINDWARD ISLANDS. **Dominica:** vicinity of Jean, NE of Salisbury (NW1561), *Ernst* 1818 (US).

COLOMBIA. **Amazonas:** Araracuara, Rio Caquetá (SW0072), *Londoño et al.* 1541 (K). **Antioquia:** Guatapé, Vereda Santa Rita (NW0675), *Escobar et al.* 8210 (K). **Nariño:** Municipio Barbacoas, Vereda El Barro (NW0178), *Franco et al.* 5167 (NY). **Putumayo:** Municipio Mocoa, Vereda Alto Campucana (NW0176), *Betancur et al.* 5215 (K). **Valle:** 7 km N of Caicedonia, Finca La Carmelita (NW0475), *Silverstone-Sopkin & Paz* 6943 (K).

VENEZUELA. **Carabobo:** Municipio Autonomo Mara, R. Moron (NW1068), *Diaz & Niño* 266 (K). **Yaracuy:** Serranía de Aroa, N of Urachiche (NW1069), *Meier et al.* 5651 (K).

GUYANA. Upper Takutu-Upper Essequibo Region, Acarai Mts. (NW0158), *D. Clarke et al.* 7677 (U).

FRENCH GUIANA. Saül (NW0353), *Mori & Pipoly* 15615 (K).

ECUADOR. **Cotopaxi:** Sigchos, Triunfo Grande-Sigchos (SW0078), *Ramos et al.* 6890 (MO). **Esmeraldas:** San Lorenzo, Alto Tambo (NW0078), *Quelal et al.* 439 (K). **Loja:** Cerro Uritusinga (SW0479), *Jorgensen et al.* 1120 (K). **Morona-Santiago:** 35 km N of Gualaquiza (SW0378), *Pennington & Tenorio* 10771 (K). **Orellana:** Yasuní National Park, Maxus road, km 40 (SW0076), *M. Aulestia* 2714 (K). **Pastaza:** Pastaza Cantón, Villano (SW0177), *Espinoza & Gualinga* 835 (K). **Pichincha:** Puerto Quito-La Union (NW0079), *Jaramillo* 7747 (K). **Sucumbios:** Comuna El Pilchí (SW0076), *Freire & Chavez* 5372 (K). **Zamora-Chinchipe:** Rio Nangaritzta, Campamento Shaima (SW0478), *van der Werff et al.* 13014 (K).

PERU. **Amazonas:** Florída-Rioja km 31 (SW0577), *Pennington & Daza* 16807 (K, MOL). **Huánuco:** junction of R. Pachitea & R. Yuyapichis, Panguana (SW0974), *Morawetz & Wallnöfer* 113-21085 (K). **Madre de Dios:** Manu, Manu National Park, Cocha Cashu (SW1171), *Chatrou et al.* 128 (K). **Piura:** Montaña de Cuyas, 8 km NE of Ayabaca (SW0479), *Gentry et al.* 75061 (K). **San Martín:** Rioja Prov., Pedro Ruiz to Moyabamba km 390 (SW0577), *D.N. Smith & Vásquez* 4738 (K). **Ucayali:** Prov. Purus, Rio Curanja (SW1071), *Graham & Schunke* 902 (K).

BRAZIL. **Acre:** Municipio Tarauaca, Seringal Vitoria Velha (SW0870), *Figueiredo et al.* 933 (NY). **Amazonas:** Municipio Atalaia do Norte, R. Javari, Estirão de Equador (SW0471), *Cid Ferreira et al.* 9904 (K). **Bahía:** Ilheus to Itabuna km 22 (SW1439), *Hage & Brito* 2198 (K). **Distrito Federal:** APA de Cafuringa, Fazenda Palestina (SW1547), *Pereira* 2247 (K). **Goias:** Chapada dos Veadeiros, Fazenda Pai José (SW1447), *Mendonça & Cesar* 2224 (K). **Mato Grosso:** Serra das Araras (SW1556), *Dubs* 1293 (K). **Mato Grosso do Sul:** Municipio Bonito, Cachoeira do Rio Aquadaban (SW2156), *Hatschbach et al.* 74130 (K). **Pará:** Lageira (SW0054), *Strudwick et al.* 3855 (K).

BOLIVIA. **La Paz:** Iturrealde, Santa Fe (SW1368), *De Walt et al.* 765 (K). **Santa Cruz:** Ichilo, SE of Buena Vista (SW1763), *Nee* 45246 (K).

PARAGUAY. **Alto Paraná:** Estância Rio Bonito (SW2554), *Zardini & Vera* 42606 (K). **Amambay:** Estância la Serrana (SW2255), *Zardini & Cardozo* 45095 (K). **Caazapa:** Estância

Golondrina, Ypeti (SW2555), *Zardini & Hellman* 49000 (K). **Guaira**: Cordillera de Ybytyruzú (SW2456), *Zardini & Aguayo* 14074 (K). **San Pedro**: Yaguarete (SW2355), *Zardini & Garcete* 43331 (K).

ARGENTINA. **Misiones**: Eldorado, banks of R. Paraná (SW2654), *Burkart* 14558 (K).

Although this species has the typical flower and fruit structure of *Guarea*, it is probably the easiest species to identify, even in a vegetative state. This is due to the characteristic leaf venation, with obscure and widely separated tertiary veins, the glabrous ovary and smooth lenticellate fruit. Its rather isolated position within *Guarea* is confirmed by the ITS phylogeny.

11. *Guarea jamaicensis* Proctor, Bull. Inst. Jamaica, Sci. Ser. 16: 19, t. 6 (1967); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 320, fig. 66 (1981). – Type: Jamaica, Parish of St. James, White Rock Hill, fl., *Proctor* 23188 (holo IJ; iso GH, NY). **Fig. 66A.**

Abbreviated description. Young shoots and inflorescences minutely appressed puberulous, leaves with a terminal bud showing intermittent growth, leaflets (2–)3–4(–5) pairs, 6.5–8.5 × 3–4 cm, elliptic to broadly oblanceolate, coriaceous, glabrous, venation eucamptodromous to brochidodromous, secondaries 9–10 pairs, inflorescence axillary, 2–3 cm long, a few-flowered raceme or panicle, petals 4, c.8.5 mm long, valvate, staminal tube 6–6.5 mm long, 2.5–3 mm broad, anthers 8, ovary 3–4-locular, locules with 1–2 collateral or superposed ovules, capsule 1.3–1.6 cm diam., globose, smooth, sparsely appressed puberulous, 3–4-valved, pericarp c.1 mm thick, valves with 1–2 collateral seeds.

Field characters. Fruiting recorded in February, July and November.

Distribution and ecology. Jamaica, on forested limestone hills, between 700 m and 1000 m altitude.

Additional collections examined. JAMAICA. St. Ann Parish, Broom Hall Woods (NW1877), *Gentry et al.* 28434 (K); Clarendon, Cecil Lindo's Estate (NW1877), *Goodfriend* s.n. (F); St. Ann, W of Prickly Pole P.A., *Proctor* 38428 (NY).

A genetically isolated species, possibly related to *Guarea sphenophylla* (based on their geography and morphology), but no ITS sequence data were available from the latter to confirm this hypothesis.

12. *Guarea pterorhachis* Harms, Notizbl. Bot. Gart. Berlin-Dahlem 9: 141 (1924); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 326, fig. 68 (1981). – Type: Peru, Loreto, Middle Ucayali, fl., *Tessmann* 3164 (holo B, destroyed; lecto G, designated here; isolecto NY).

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 326 (1981).

Abbreviated description. Young shoots and inflorescences sparsely appressed puberulous, leaves with a terminal bud showing intermittent growth, petiole and rhachis

broadly winged, leaflets 2–6 pairs, 10–34 × 3.5–11 cm, oblong to narrowly elliptic, chartaceous to coriaceous, glabrous, higher order venation obscure, inflorescence 35–80 cm long, a much-branched thyrse with widely spreading branches, the lower ones up to 70 cm long, flowers in dense subfasciculate clusters, petals 4, valvate or slightly imbricate towards the apex, (3.5–)4–5 mm long, anthers (7–)8, ovary 2-locular, locules with 2 superposed ovules, glabrous, capsule 1.5–2 cm long, ellipsoid and borne obliquely on the pedicel (when 1-seeded) or bilobed and constricted between the valves (when 2-seeded), smooth, glabrous, 2-valved, pericarp 0.75–1 mm thick, seed solitary or 1 in each valve.

A distinct species, differing from all others by the broadly winged leaf rhachis. It shares some floral characters with *Guarea silvatica*, such as the slightly imbricate petals and 2-locular glabrous ovary. The ITS phylogeny confirms its isolated position at the end of a long branch and sister to all other South American species.

Key to the subspecies of Guarea pterorhachis

- 1a. Venation eucamptodromous, the secondary veins gradually diminishing and disappearing below the margin _____ **12a. *G. pterorhachis* subsp. *pterorhachis***
 1b. Venation brochidodromous, the secondary veins joining just below the margin in a strong ± straight submarginal vein running parallel to the margin _____
 _____ **12b. *G. pterorhachis* subsp. *submarginalis***

12a. *Guarea pterorhachis* subsp. *pterorhachis*. Fig. 52C.

Distribution and ecology. Nicaragua, Costa Rica and Panama, Amazonian Colombia, Ecuador (including the Pacific drainage (Canar)), Peru, Bolivia and western Amazonian Brazil. A species of lowland and montane rain forest up to 1000 m altitude, mostly on non-flooded land but occasionally recorded from periodically flooded forest in western Amazonia.

Representative additional collections. NICARAGUA. **Chontales:** foot of Loma San Gregorio, *Sandino* 5169 (K). **Matagalpa:** Macizos de Peñas Blancas, SE side, Quebrada el Quebradon (NW1383), *Stevens et al.* 21384 (K). **Zelaya:** Municipio de Siuna, Caño el León (NW1384), *Ortiz* 726 (K).

COSTA RICA. **Alajuela:** Monteverde Reserve, Rio Peñas Blancas (NW1084), *Bello* 1631 (INB, K). **Guanacaste:** Rincón de la Vieja National Park (NW1085), *Rivera & Dennis* 1103 (K). **Limón:** Hitoy Cerere Biological Reserve (NW0983), *Herrera & Chacon* 2343 (K). **Puntarenas:** Cantón de Golfito Jimenez, Alto de Carbonera (NW0883), *Herrera* 4312 (CR, K); Cantón de Osa, near Dominical (NW0983), *Fernandez* 511 (INB). **San José:** Puriscal, Cerro Pilon (NW0984), *Morales* 3938 (INB).

PANAMA. **Colon:** Santa Rita Ridge (NW0979), *McPherson* 9180 (K). **Herrera:** W of Las Minas, Montosa de Chepo (NW0780), *McPherson* 10949 (K).

ECUADOR. **Cañar:** E of Manta Real (SW0279), *Cornejo & Bonifaz* 3680 (K). **Morona-Santiago:** Cordillera de Condor, Centro Shuar Warints (SW0378), *Kajekai et al.* 13 (K). **Orellana:** 30 km NW of Coca, Huashito (SW0077), *Pennington* 10593 (K). **Pastaza:** Rio

Pastaza, between Chiriboga and Apachi Entza (SW0276), *Ollgaard et al.* 35166 (K). **Zamora-Chinchipe**: Nangaritza (SW0478), *Quizhpe et al.* 466 (K).

PERU. **Amazonas**: Bagua Province, Yamayakat (SW0478), *Vásquez & Jaramillo* 20317 (K). **Huánuco**: Yuyapichis, Puerto Inca, DANTAS (SW0975), *Tello* 376 (K). **Ucayali**: Purus, Rio Curanga, Colombiana (SW1071), *Graham & Schunke* 147 (K).

BRAZIL. **Acre**: Fazenda Bom Sossego (SW0773), *Campbell et al.* 9509 (K). **Rondonia**: Municipio de Costa Marques, Chapada dos Parecis (SW1162), *Cid et al.* 4525 (K).

BOLIVIA. **Beni**: Prov. Ballivian, Serrania Pilon Lajas (SW1567), *Solomon* 13899 (K). **Santa Cruz**: Ichilo, S of San Rafael (SW1763), *Nee & Saldias* 36877 (K).

12b. *Guarea pterorhachis* subsp. *submarginalis* T.D.Penn., subsp. nov. Figs 10, 52D.

Ab subspecie *pterorhachidi* venatione brochidodroma, nervi submarginali valido differt. – Type: Colombia, Choco, Quebrada Argueta, S of Rio Mecana [NW0677], fl., *Juncosa* 1717 (holo K; iso MO).

Distribution and ecology. Pacific drainage of Colombia, known from Antioquia, Choco and Valle. It has the same ecology as the typical subspecies and is present in wet lowland and montane rain forest from sea level to 1400 m altitude. It is, however, geographically distinct from the typical subspecies, which in Colombia is known only from the extreme southeast corner of the Amazon.

Field characters. Tree to 15 m high with cream-coloured flowers. Flowering and fruiting recorded March to April.

Collections examined. COLOMBIA. **Antioquia**: ‘Las Orquideas’ National Park track to San Mateo (NW0676), *Cogollo et al.* 3321 (MO), Rio Venados (NW0676), *Cogollo et al.* 3573 (MO); Murri la Blanquita, Rio Murri (NW0676), *Gentry et al.* 75806 (MO); Municipio Frontino, Nutibara (NW0676), *Luteyn et al.* 12127 (K). **Choco**: Bahía Solan Municipio, Corregimiento El Valle (NW0676), *Espina et al.* 2620 (K, MO); Municipio San José del Palmar, vereda la Badea (NW0476), *Franco et al.* 1804 (MO); area of Baudo, Rio Baudo (NW0477), *Fuchs & Zanella* 22074 (MO, NY, US). **Valle**: Río Calima, La Trojita (NW0477), *Cuatrecasas* 16598 (F, US); Municipio Buenaventura, Campamento El Chanco (NW0476), *Devia* 1209 (MO); Bajo Calima Concesion, 16 km NW of Buenaventura (NW0477), *Faber-Lagendoen & Renteria* 1044 (K); Bahía Malaga near Juanchaco, *Gentry et al.* 53365 (K, MO); Concesión Pulpapel/Buenaventura, Bajo Calima (NW0377), *Monsalve* 1929 (MO).

This subspecies was first collected by *Cuatrecasas* (no. 16598) in 1944 and noted as possibly distinct in *Flora Neotropica* (Pennington *et al.*, 1981: 329). The collection of complete material since 1981 enables its recognition as a subspecies of *Guarea pterorhachis*. The flowers and fruit do not differ from those of the typical subspecies but the brochidodromous venation with a well-defined submarginal vein is consistently different. It is also geographically distinct from the typical subspecies.

13. *Guarea caulobotrys* Cuatrec., Fieldiana, Bot. 27(1): 69 (1950); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 345 (1981). – Type: Colombia, Dept. del Valle, Costa del Pacífico, R. Naya [NW0377], fl., *Cuatrecasas* 14103 (holo F; iso COL). Figs 11, 52E.

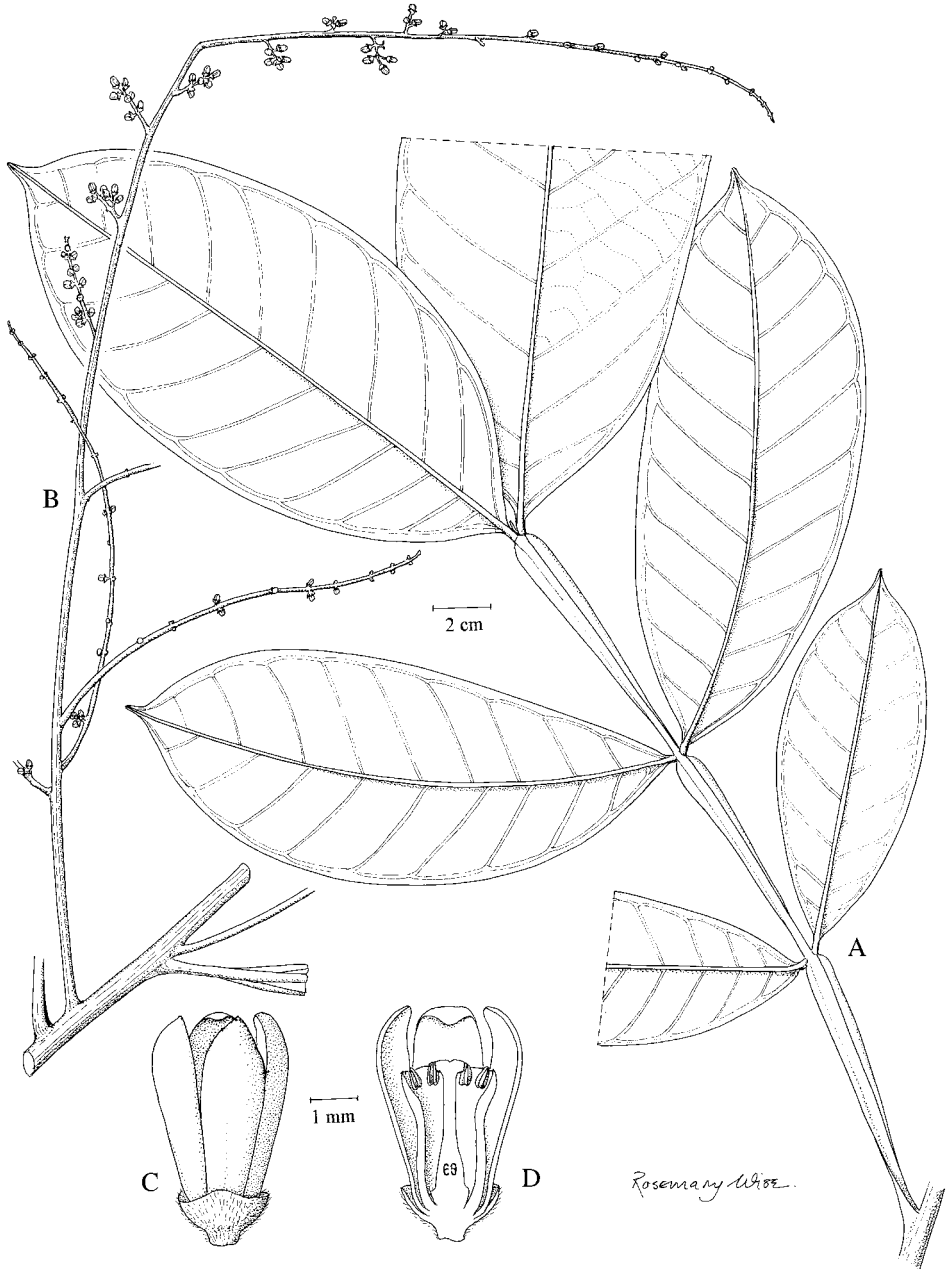


FIG. 10. *Guarea pterorhachis* Harms subsp. *submarginalis* T.D.Penn. A, leaf; B, inflorescence; C, flower; D, half-flower. (A, *Gentry et al.* 53365; B–D, *Juncosa* 1717).

Young shoots minutely appressed puberulous to tomentose, stout, c.1 cm diam., and often hollow, eventually scaling and suberous, scales c.2–3 × 0.5 mm. *Leaves* pinnate with a terminal bud with intermittent growth, petiole 20–25 cm long, channelled at

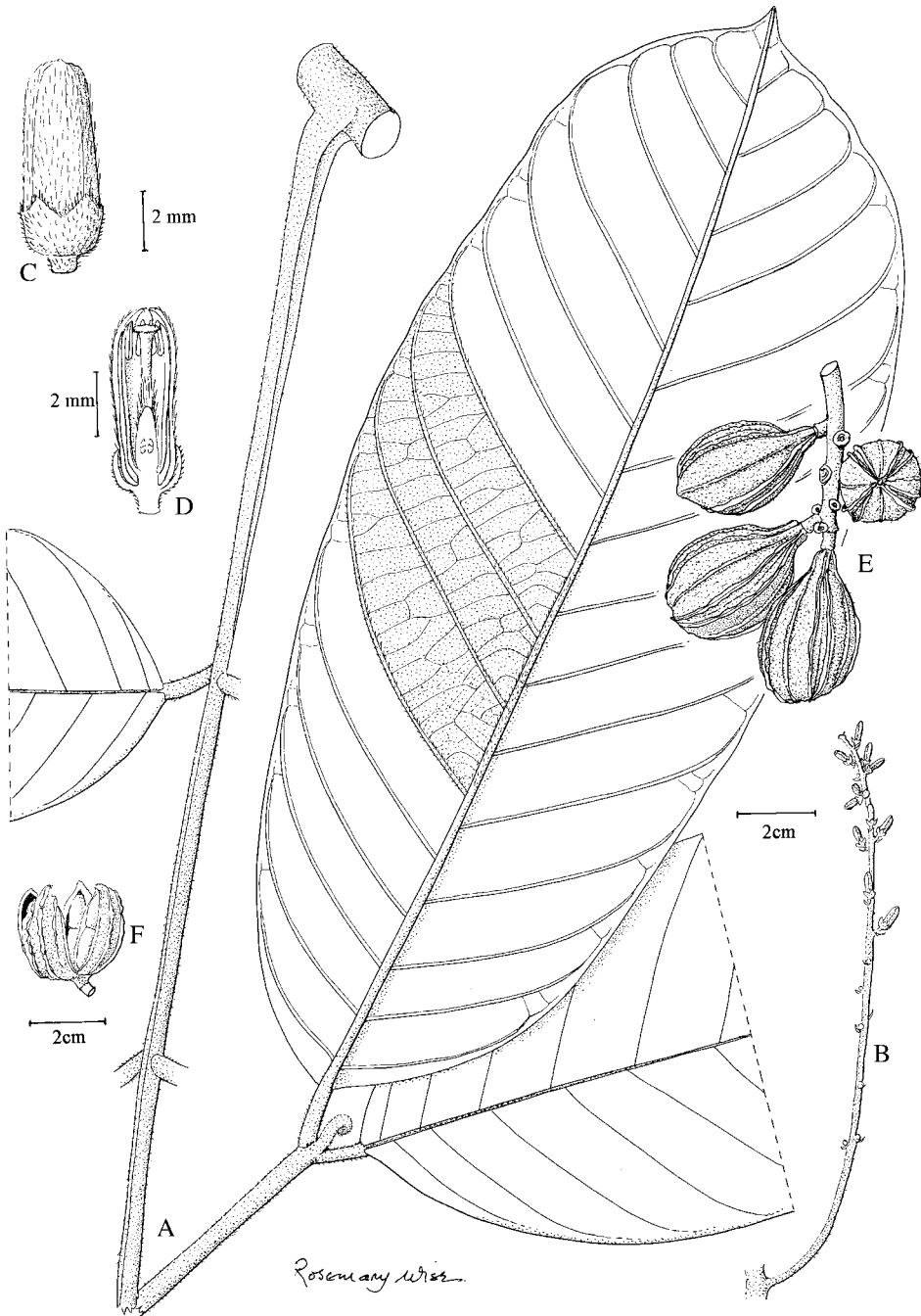


FIG. 11. *Guarea caulobotrys* Cuatrec. A, leaf; B, inflorescence; C, flower bud; D, half-flower; E, infructescence; F, dehiscent fruit. (A, E, *Monsalve* 1673; B–D, *McPherson* 11866; F, *Juncosa* 1233).

the base to semiterete at the apex, pubescent to tomentose, rhachis up to 70 cm long, terete, pubescent to tomentose; petiolute swollen, 1–10 mm long, pubescent to tomentose. *Leaflets* opposite, 3–5 pairs, 28–46.5 × 8.9–17.5 cm, broadly oblong to broadly elliptic, apex acute to acuminate or obtusely cuspidate, base acute to obtuse or truncate, chartaceous to coriaceous, upper surface glabrous or with residual indumentum on the midrib, lower surface pale tomentose on midrib and veins, sparsely soft pubescent on the lamina, or eventually glabrous, minute raised dots usually visible on upper surface (× 10), not glandular-punctate or -striate; venation mostly eucamptodromous, sometimes brochidodromous towards the apex, midrib sunken on the upper surface, secondaries 16–21 pairs, ascending, straight and parallel, intersecondaries short or absent, tertiaries oblique, sometimes prominent below. *Inflorescence* cauliflorous, 5–25 cm long, a raceme or slender panicle with a few short lateral branches and thyrsoid flower clusters, flower clusters subtended by a short lanceolate bract c.2 mm long, pubescent to tomentose; pedicel c.1 mm long. *Calyx* patelliform to cyathiform, 1.5–2.5 mm long, 4-lobed to halfway or more, the lobes broadly ovate and often obtusely cuspidate at the apex, sparsely pubescent outside, glabrous inside. *Petals* 4, c.12 × 2 mm, strap-shaped, apex acute, free, valvate, sericeous outside, glabrous inside. *Staminal tube* c.9 mm long, c.3 mm broad, margin undulate, glabrous; anthers 8–9, c.1.5 mm long, narrowly oblong, dehiscent, glabrous. *Nectary* c.2 mm long, a stout stipe expanded into a collar below the ovary, glabrous. *Ovary* ovoid, c.3 mm long, 4-locular, locules with 2 superposed ovules, densely strigose, style c.2 mm long, style-head discoid. *Capsule* 2.5–4 cm long, 1.7–2.5 cm broad, ovoid, obovoid or pyriform, apex rounded, base obtuse, 4-valved, each valve with 3 irregular thick, longitudinal, torulose ribs, tending to anastomose at the apex, ribs 2–3 mm high, pericarp 3–4 mm thick (without the ribs), minutely puberulous to shortly tomentose, indumentum intermixed with sparser longer hairs, valves with 2 superposed seeds and not constricted between the seeds. *Seeds* c.10 × 6 mm, plano-convex, completely surrounded by a thin fleshy sarcotesta. *Seed coat* thin and fleshy.

Field characters. Unbranched or sparsely branched treelet to 8 m high and 12 cm diam.; bark reddish brown, scaling and slightly suberous; with a terminal cluster of leaves up to 1 m long; cauliflorous with creamish white flowers; and the fruit maturing dark red. Flowering recorded in December and January, fruiting in April and October.

Distribution and ecology. Pacific coast of Colombia (Choco, Nariño and Valle) to Panama (provinces of Panamá and San Blas) in wet lowland rain forest up to 350 m altitude.

Collections examined. PANAMA. **Panamá:** El Llano–Carti road 20 km N of turnoff (NW0978), Churchill 3826 (MO). **San Blas:** El Llano–Carti road, 16.5 km N of Panamerican highway (NW0978), Folsom 2612 (MO); San Blas–Panamá border on Kuna divide trail (NW0979), McPherson 11866 (MO); San Blas boundary trail on El Llano–Carti road (NW0979), McPherson & Merello 8184 (K); Continental divide trail to W from El Llano–Carti road (NW0978), Nevers & Herrera 4474 (MO).

COLOMBIA. **Chocó:** Municipio Istmina, Alto Rio San Juan (NW0576), *Espina et al.* 1399 (K, MO); Tutunendo to Icho (NW0576), *Juncosa* 1233 (K, MO). **Nariño:** Municipio de Mosquera, quebrada La Barrera (NW0278), *Romero-Castañeda* 5519 (COL). **Valle:** R. Yurumanguí (NW0377), *Cuatrecasas* 15739 (F); Bajo Calima Concession, 16 km N of Buenaventura (NW0377), *Faber-Langendoen et al.* 224 (K); Concesión Pulpapel/Buenaventura (NW0377), *Monsalve* 1673 (MO).

This species is morphologically close to *Guarea fistulosa* (Amazonian drainage of Colombia, Ecuador and Peru and Panama). The species share similar vegetative structure of stems and leaves, including the hollow twigs, and their flowers and fruit are also very similar in size and number of parts. The only differences we can find are the scaly twigs of *Guarea caulobotrys* (smooth in *G. fistulosa*), presence of minutely raised dots on the upper leaf surface of *Guarea caulobotrys* (absent in *G. fistulosa*), and a slight difference in the thickness of the fruit ribs. However, this close morphological similarity is not reflected in the ITS phylogeny which indicates that it occupies a basal position, sister to the rest of the South American clade, whereas *Guarea fistulosa* is remote from it on one of the ultimate branches.

14. *Guarea zepivae* T.D.Penn., sp. nov. Figs 12, 51B.

Guarea gracili affinis sed petiolo longiore, nervis secundariis 12–13, foliolis pubescentibus, capsula laevi differt. – Type: Brazil, Mato Grosso, Municipio Novo Mundo, Parque Estadual Cristalino, fl., *Sasaki, Biggs, Silveira, Philippsen & Bessa* 2089 (holo SPF n.v.; iso K).

Young shoots softly pubescent, 5–7 mm diam., smooth, indumentum persistent. *Leaves* pinnate with a non-active terminal bud, petiole 10–13.5 cm long, semiterete, softly pubescent, indumentum persistent, rhachis 12.5–25 cm long, semiterete and slightly channelled above to terete at the apex, softly pubescent; petiolule 5–7 mm long, pubescent. *Leaflets* 4–5 pairs, opposite, 17.5–25.5 × 5–8.3 cm, elliptic or oblanceolate, apex acuminate, base acute or narrowly attenuate, chartaceous, upper surface shortly pubescent on midrib and secondary veins and with scattered pubescence on the lamina, not glandular-punctate or -striate, leaves drying pale green; venation eucamptodromous, midrib slightly sunken on the upper surface, secondaries 12–13 pairs, steeply ascending, slightly arcuate and slightly convergent, intersecondaries short or absent, tertiaries oblique, obscure. *Inflorescence* on twigs below the leaves, 2–5 cm long, a small panicle with short lateral branches to 3–4 mm long, pubescent; pedicel 1–1.5 mm long, pubescent. *Flowers* subtended by a small bract 0.5–1 mm long. *Calyx* c.2.5 mm long, cup-shaped, shallowly and irregularly lobed to 1/4 its length, sparsely pubescent outside, glabrous inside. *Petals* 4, 7.5–8 mm long, 1–1.5 mm broad, strap-shaped, apex acute, densely appressed pubescent outside (pale whitish hairs), glabrous inside. *Staminal tube* c.6.5 × 2 mm, cylindrical, margin undulate to shortly lobed, glabrous; anthers 8, c.1 mm long, glabrous. *Nectary* a stout stipe c.1 mm long, expanded below the ovary, glabrous. *Ovary* c.2 mm long, ovoid, 4-locular, locules with 1 ovule, sparsely strigose, style 3–3.5 mm long, glabrous, style-head discoid, slightly

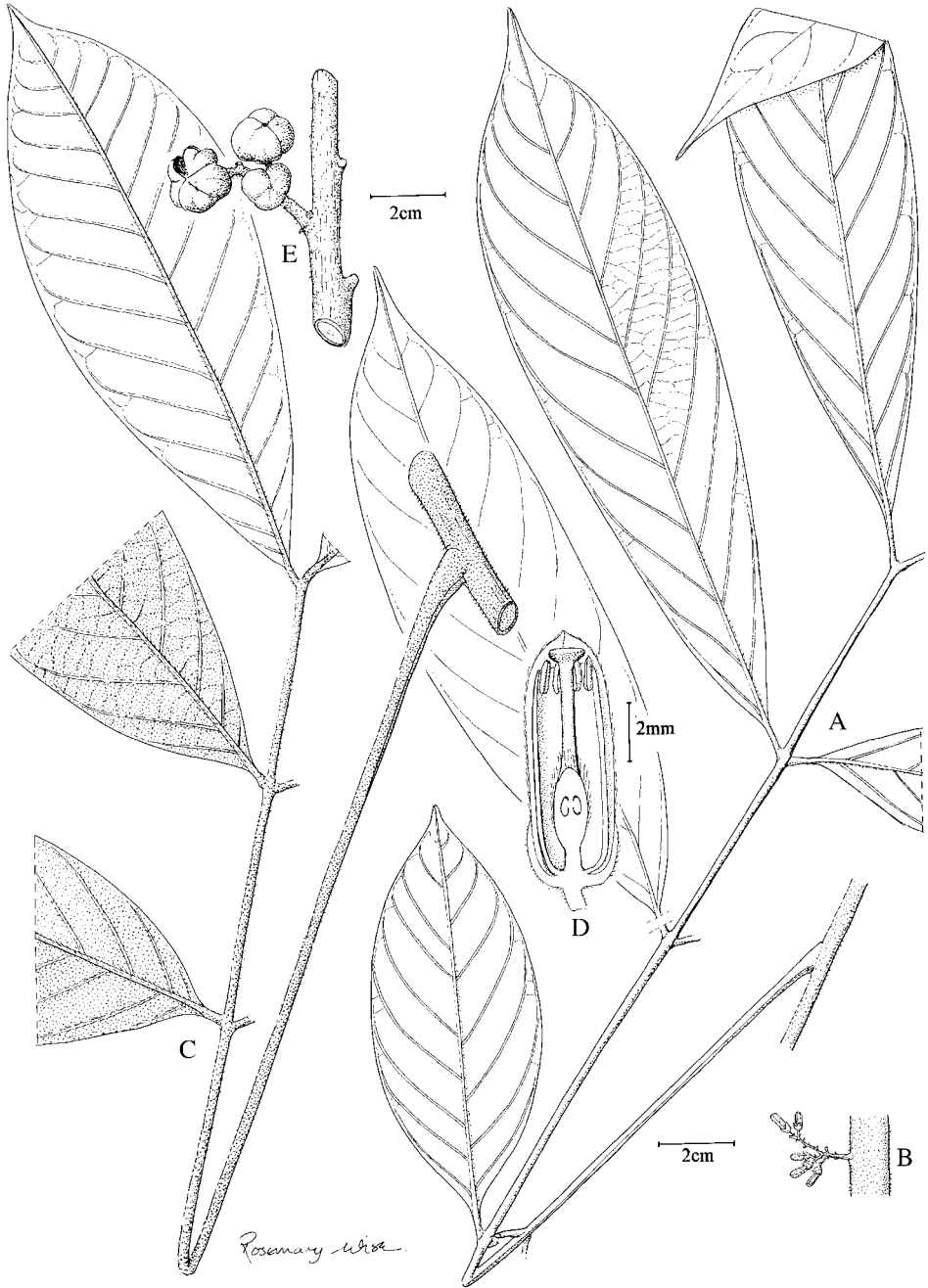


FIG. 12. *Guarea zepivae* T.D.Penn. A, leaf; B, inflorescence; C, leaf with indumentum on lower surface; D, half-flower; E, fruit. (A, B, D, Sasaki et al. 2089; C, E, Sasaki et al. 1737).

exceeding the anthers. *Capsule* 1.1–1.3 cm long, 1.2–1.5 cm broad, oblate to globose, apex truncate, base truncate or obtuse, (3–)4-valved, valves 1-seeded, smooth, sparsely and coarsely pubescent at first, glabrous at maturity, pericarp c.1 mm thick. *Seed* 8–9 mm long, shaped like the segment of an orange, surrounded by a thin oily sarcotesta.

Field characters. Treelet to 6 m high, with whitish flowers and red fruit. Flowering recorded in February, fruit maturing in June.

Distribution and ecology. An understory treelet in transitional seasonal forest with an open canopy 10–20 m high, and emergents to 35 m high, over non-flooded sandy land, below 300 m altitude. At present known only from the Parque Estadual Cristalino, Mato Grosso, Brazil.

Collections examined. BRAZIL. **Mato Grosso:** Município de Novo Mundo, Parque Estadual Cristalino (SW0955), Sasaki *et al.* 1670 (K), 1737 (K).

Guarea zepivae is morphologically closest to two other southeast Brazilian species, *G. gracilis* and *G. pendula*, and all share similar small flowers with 4 petals, 8 stamens, 4-locular ovary with uniovulate locules, and small 4-valved capsule. *Guarea zepivae* differs from *G. gracilis* in the following characters: petiole 10–13 cm long (2–4 cm long in *G. gracilis*), leaflets 17.5–25.5 cm long (9–13.5 cm long in *G. gracilis*), secondary veins 12–13 pairs (6–8 pairs in *G. gracilis*), leaflets pubescent (subglabrous in *G. gracilis*), capsule smooth (capsule prominently ribbed in *G. gracilis*). *Guarea pendula* has leaflets bearing numerous minute red papillae on the lower surface, whereas these are absent in *G. zepivae*. It also differs in having fewer secondary veins and in its pyriform costate capsule.

The morphological resemblance is not reflected in the ITS phylogeny which shows *Guarea zepivae* to be embedded with other Amazonian species, whereas *G. gracilis* and *G. pendula* are embedded in a small group of coastal Brazilian species.

This species is named after José (Zé) H. Piva, field technician with the Kew Cristalino Project, skilled plant identifier and self-taught botanist, co-author of *Vegetação e Plantas do Cristalino* (Sasaki *et al.*, 2010).

15. *Guarea sprucei* C.DC. in Mart., Fl. Bras. 11(1): 196, t. 58 (1878); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 334 (1981). – Type: Brazil, Amazonas, R. Negro, near São Gabriel da Cachoeira [SW0067], fl., Spruce 2240 (holo G-DC; iso BM, K, M, NY, OXF, P). **Figs 13, 48B.**

Young shoots densely golden-tomentose to villose, massive, 2–3 cm diam., soon developing a strongly suberous, fissured bark 5–10 mm thick. *Leaves* pinnate with a terminal bud showing indeterminate growth, petiole 5–10 cm long, channelled and slightly winged at the base to semiterete at the apex, tomentose, rhachis up to 80 cm long, semiterete, tomentose; petiolule very short, tomentose. *Leaflets* opposite, 3–8 pairs, 30–38 × 11–14 cm, lower ones much smaller, broadly oblong, apex acute to obtusely cuspidate, base truncate to slightly cordate, coriaceous and strongly bullate,

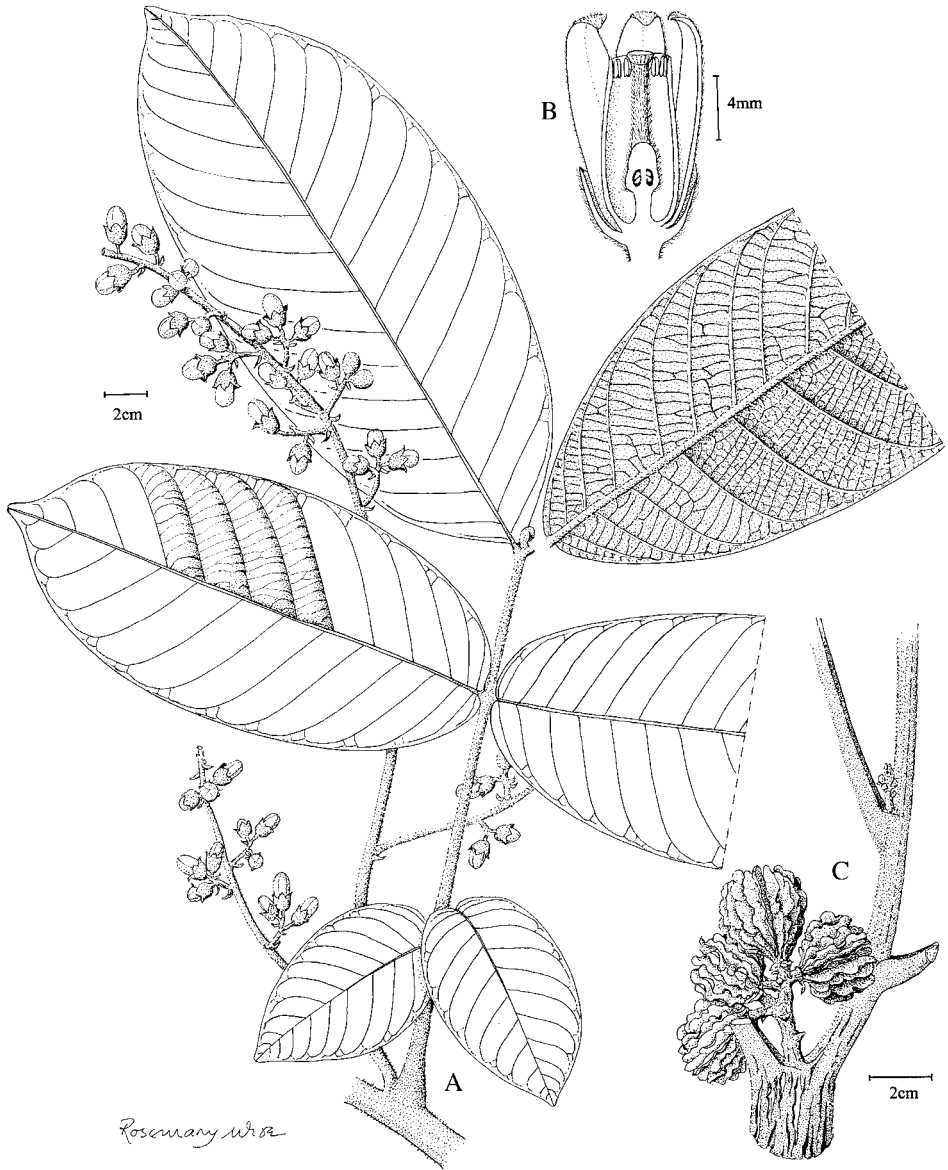


FIG. 13. *Guarea sprucei* C.DC. A, habit; B, half-flower; C, infructescence. (A, B, *Spruce* 2240; C, *Cid et al.* 1567).

upper surface with tomentose midrib and veins at first, becoming glabrous, lower surface with tomentose to villose midrib and veins, and pubescent lamina, hairs intermixed with minute red papillae, not glandular-punctate or -striate; venation eucamptodromous, midrib sunken on the upper surface, secondaries 18–23 pairs, shallowly ascending, parallel, straight or slightly arcuate, lowermost secondaries

often slightly divergent, intersecondaries very short, tertiaries oblique, parallel, sunken on the upper surface, raised strongly on the lower surface; higher order reticulum prominent on the lower surface. *Inflorescence* axillary or on twigs below the leaves, 15–30 cm long, a laxly-branched panicle, the lowest lateral branches to 12 cm long, golden-tomentose, flower clusters subtended by small lanceolate bracts 2–3 mm long; pedicel 1–1.5 mm long. *Calyx* 6–7 mm long, cyathiform, irregularly 3–5-lobed, golden-tomentose. *Petals* 5, valvate, 14–15 mm long, 3.5–4.5 mm broad, oblong, apex acute, golden-sericeous outside, glabrous inside. *Staminal tube* slightly narrowed at the throat, 11–12 mm long, 3–4 mm broad, margin undulate, glabrous; anthers 10–11, c.1.8 mm long. *Nectary* a stout stipe expanded at the apex to form a ring below the ovary, c.2.5 mm long, glabrous. *Ovary* strongly longitudinally ribbed, 6–8-locular, locules with 2 superposed ovules, densely strigose, style stout, strigose, style-head discoid. *Capsule* 3.5–4 cm long and broad, obovoid, apex truncate, base obtuse, 6–8-valved, each valve with 3 longitudinal convoluted and anastomosing ribs or wings to 6 mm deep, golden-velutinous, valves with 1–2 superposed seeds, pericarp 2–3 mm thick (excluding the wings); immature seeds only.

Field characters. A slender tree to 30 m high, with whitish flowers. Flowering is recorded in March and October, with mature fruit in July.

Distribution and ecology. Upper Rio Negro, Amazonas and along the Rio Trombetas in Pará, Brazil in lowland non-flooded rain forest.

Collections examined. BRAZIL. Amazonas: Rio Negro, São Gabriel da Cachoeira, above confluence with R. Uaupés (NW0067), *Daly et al.* 5452 (K, NY). Pará: Município Oriximiná, R. Trombetas, Lago Erepeçu (SW0156), *Cid et al.* 1567 (K, NY, US); Município Oriximiná, R. Trombetas, Lago Mucura (SW0155), *Cid et al.* 1750 (K, NY, US); Município Oriximina, R. Trombetas, Porto Trombetas (SW0156), *Cid et al.* 1962 (NY).

The Pará collections are included in this species with some reservations as they differ from those of the type locality in some minor characters such as the slightly longer petiolules and the slightly shorter indumentum. However, at this time, with so few collections available, there is no justification for regarding them as specifically distinct.

The ITS phylogeny places this species with two other large-flowered species with prominently ribbed or winged capsules (*Guarea carinata* and *G. cristata*).

16. *Guarea carinata* Ducke, Trop. Woods 76: 16 (1943); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 342, fig. 72 (1981). – Type: Brazil, Amazonas, Esperança (mouth of R. Javari), fr., *Ducke* 1060 (holo RB; iso K, MG, NY, US). **Fig. 48C.**

Abbreviated description. Young shoots and inflorescences densely golden tomentose, twigs becoming suberous and fissured, leaves with a terminal bud showing intermittent growth, leaflets up to 7(–10) pairs, 14–27 × 4.5–10(–12) cm, usually oblong, less frequently elliptic or oblanceolate, chartaceous to thinly coriaceous,

upper surface with pubescent midrib, lower surface coarsely pubescent, denser on the veins, secondary veins (14–)16–20 pairs, inflorescence axillary or in the axils of fallen leaves, 2–10 cm long, unbranched or with short lateral branches, flowers in small sessile clusters, subtended by short bracts, petals 4(–5), valvate, 14–17 mm long, densely golden strigose, staminal tube 11–13 mm long, 3–4(–5) mm broad, anthers 8–11, ovary (4–)5–6(–9)-locular, locules with 2 superposed ovules, capsule 3–4.8 cm long, 3–4.2 cm broad, usually pyriform, rarely depressed-globose, 5–6(–9)-valved, valves shallowly to prominently 3-ribbed, the central ribs often larger and branching and anastomosing above, tomentose or pubescent with age, pericarp 4–6 mm thick, valves with 2 superposed seeds.

Distribution and ecology. Amazonian Ecuador, Peru and Brazil, Guyana, Surinam, not yet recorded from Amazonian Colombia, but almost certainly present there. In non-flooded lowland and lower montane rain forest, up to 1000 m altitude in Ecuador.

Additional collections examined. GUYANA. Bartica-Potaro 107 miles, Potaro River, Mahdia (NW0559), *FDBG* 3807 (F 1071) (K).

ECUADOR. **Napo:** Tena Cantón, Jatun Sacha Biological Station (SW0177), *Palacios et al.* 10441 (MO), *Zuleta* 10 (K); Loreto, slopes of Volcán Sumaco (SW0077), *Freire & Cerda* 149 (K).

PERU. **Loreto:** Alto Amazonas, Andoas (SW0276), *Gentry et al.* 29714 (K); Prov. Requena, Jenaro-Herrera (SW0473), *van der Werff et al.* 10023 (K).

BRAZIL. **Acre:** Upper R. Moa, near Fazenda Arizona (SW0773), *Campbell et al.* 6588 (K), Reserva INCRA Santa Luzia (SW0772), *Campbell et al.* 6808 (K), 7243 (K), 7478 (K), 7663 (K). **Amazonas:** Municipio de Novo Aripuana, BR 230, 400 km from Humaita (SW0760), *Cid Ferreira* 5974 (K, NY); Distrito Agropecuario, Reserva 1501 (km 41), (SW0259), *Mori et al.* 21325 (US); Municipio de Manaus, BR 174, km 64 (SW0259), *Nee* 42702 (K), 42759 (NY, US); Distrito Agropecuario, 90 km NNE of Manaus (SW0259), *Oliveira et al.* 465 (NY). **Mato Grosso:** Municipio Novo Aripuana, Rod. do Estanha km 120 (SW0961), *Cid Ferreira* 5670 (K). **Rondonia:** Porto Velho, Represa Samuel (SW0963), *Thomas et al.* 4973 (NY), 4987 (K).

The Guyana collection (*FDBG* 3807) is included with reservations, due to the lack of fruit, and the coarser, more hispid indumentum and strongly impressed midrib and secondary veins. The floral structure agrees with that of *Guarea carinata*.

17. *Guarea cristata* T.D.Penn. in T.D.Penn. et al., *Fl. Neotrop.* 28: 329, fig. 69 (1981). – Type: Brazil, Amazonas 180 miles up R. Javará from Tabatinga, fl., *Pennington, Prance, Hill & Ramos* 10074 (holo INPA; iso FHO, NY). **Fig. 53A.**

Abbreviated description. Young shoots and inflorescences densely golden hirsute or villose, leaves with indeterminate apical growth, leaflets up to 7 pairs, 15–29 × 3.8–8 cm, oblanceolate, chartaceous, lower surface coarsely hirsute, venation usually brochidodromous, secondary veins 13–18 pairs, inflorescence axillary, 2–5 cm long, a densely-flowered, congested thyrses or raceme, petals 4, valvate, 16–17 mm long, densely golden-sericeous, staminal tube 14–15 mm long, 5–7 mm broad, anthers 8–11, ovary 4–6-locular, locules with 2 superposed ovules, capsule tardily dehiscent, 4–6 cm diam., ± globose, with dense fleshy convoluted longitudinal wings, (12 larger wings

10–15 mm deep, 12–20 lesser wings up to 5 mm deep) 4–6-valved, each valve with 2 superposed seeds, pericarp 2–3 mm thick (excluding the wings), coarsely pubescent.

Distribution and ecology. Amazonian Colombia, Ecuador, Peru and extreme western Amazonian Brazil, mostly recorded from lowland rain forest over infertile white sand, or occasionally on red clays.

Additional collections examined. COLOMBIA. **Amazonas:** Municipio de Leticia, Tarapaca, Amacayacu National Park (SW0370), *Rudas et al.* 2409 (MO). **Caquetá:** Araracuara (SW0072), *Duivenvoorden et al.* 2766 (K), *Gentry & Sanchez* 64987 (K).

ECUADOR. **Pastaza:** Loroacachi (SW0175), *Brandbyge & Azanza* 30688 (AAU), *Jaramillo et al.* 31111 (AAU), 31374 (AAU).

PERU. **Madre de Dios:** Tambopata, Parque Nacional Bahuaja-Sonene (SW1268), *Diaz & Ramirez* 9565 (QCNE). **Loreto:** Maynas, Quebrada Blanca Biological Station (SW0373), *Castro* 1 (K); Maynas, Mishana, R. Nanay (SW0373), *Gentry & Emmons* 38771 (K), *Gentry et al.* 31685 (NY); Constanca, Quebrada Tamshiyacu (SW0472), *Gentry et al.* 76441 (K); Allpahuayo Biological Station (SW0373), *Jaramillo & Marcos* 694 (K, MO); Requena, Jenaro Herrera (SW0473), *Spichiger & Encarnacion* 1192 (G, NY); Maynas, Puerto Almendras (SW0373), *Vásquez & Jaramillo* 4609 (K); Iquitos, Allpahuayo (SW0473), *Vásquez & Jaramillo* 16629 (MO); Maynas, Puerto Almendras (SW0373), *van der Werff et al.* 9837 (K); Requena, Jenaro Herrera (SW0473), *van der Werff et al.* 10124 (K).

18. *Guarea cinnamomea* Harms, Notizbl. Bot. Gart. Berlin-Dahlem 13: 504 (1937); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 307, fig. 62 (1981). – Type: Brazil, Amazonas, Paranagua, fl., *Krukoff* 4556 (holo B, destroyed; lecto K; isolecto A, G, NY, U). **Figs 14, 48D.**

Guarea quadrangularis M.E.Morales, Rev. Acad. Colomb. Cienc. 22: 336 (1998), **syn. nov.** – Type: Colombia, Vaupés, Caparu Biological Station, 3 km N of Lake Taraira, fl., *Defler* 291 (holo COAH).

Abbreviated description. Young shoots and inflorescences puberulous, leaves with a terminal bud showing intermittent growth, leaflets up to 11 pairs, (11.2–)15–35(–45) × (5.3–)7–11.5(–12.9) cm, usually broadly oblong, sometimes narrowly elliptic or ovate, coriaceous, glabrous above, minutely puberulous on midrib and veins below, with numerous red papillae on the lamina, secondary veins 12–17 pairs, inflorescence axillary or on twigs below the leaves, 3–15 cm long, a raceme or thyrse with lateral branches to 6 cm long, petals 4–5, valvate, 11.5–14 cm long, staminal tube 9–10 mm long, c.3 mm broad, anthers 7–9, 1.5–2 mm long, ovary 4–6-locular, locules 1-ovulate, capsule 5–6.2 cm long, ovoid or broadly pyriform, apex rounded or apiculate, tapering gradually to a short stout stipe, 4–6-valved, valves smooth or faintly 5–8-ribbed, puberulous or papillose, pericarp 4–7 mm thick, valves 1-seeded.

Distribution and ecology. Central and western Amazonian Brazil, Colombia and Peru, and with a single record from French Guiana, in lowland non-flooded rain forest.

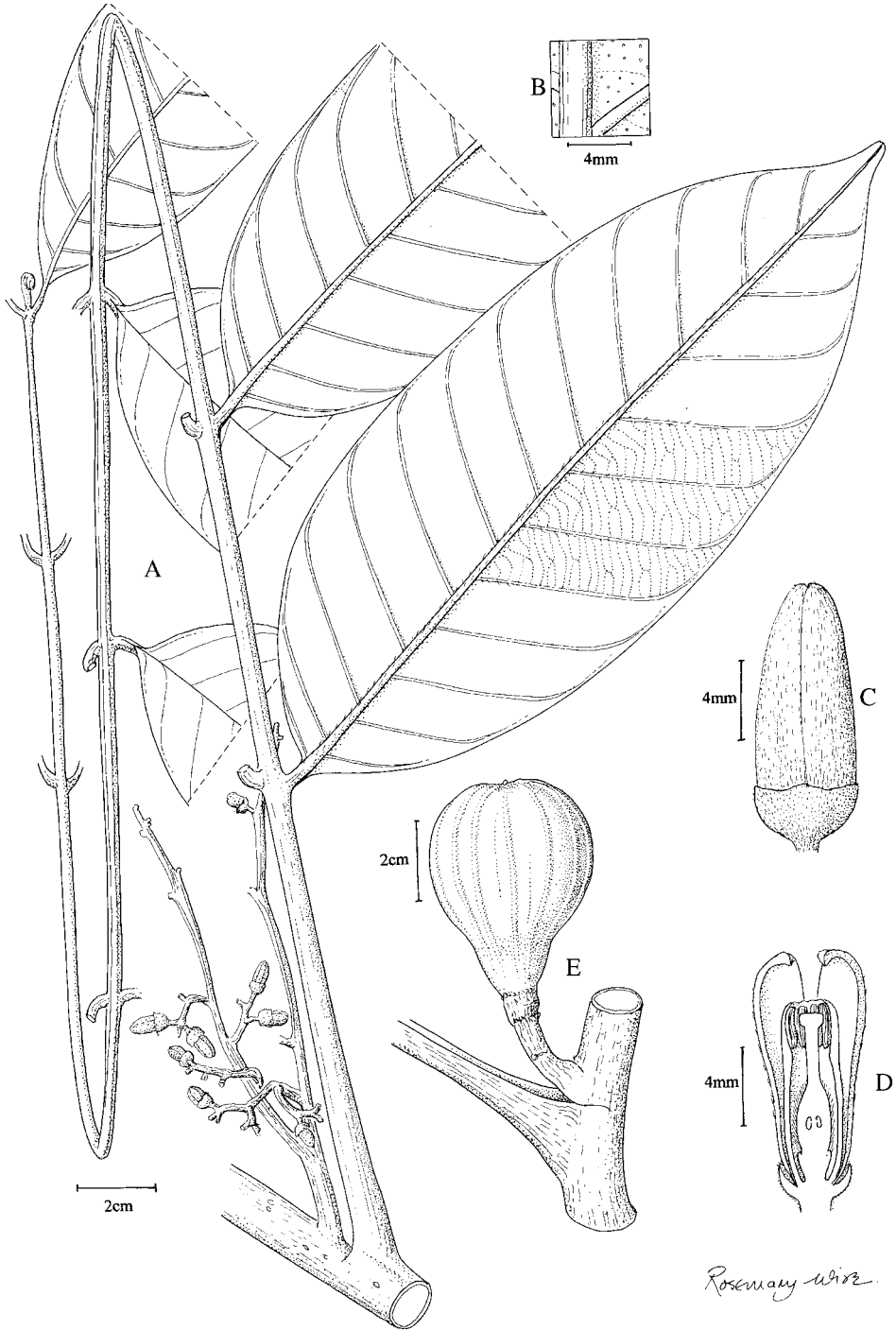


FIG. 14. *Guarea cinnamomea* Harms. A, habit; B, enlargement of leaf underside; C, flower bud; D, half-flower; E, fruit. (A–D, *Daly et al.* 4179; E, *Thomas et al.* 5362).

Additional collections examined. FRENCH GUIANA. Fleure Approuague, Rivière Matarony, Saut Magasin (NW0451), *Oldeman* B1017 (K, U).

COLOMBIA. **Vaupés:** Caparú Biol. St., N of Lake Taraira (SW0169), *Defler* 291 (COAH).

PERU. **Amazonas:** Condorcanqui Province, El Cenepa, Tutino (SW0478), *Vásquez et al.* 24209 (F). **Loreto:** Requena, Jenaro Herrera (SW0473), *Collector unknown* (Fig. 2-1/85) (K, MOL); *Pennington et al.* 17417 (K, MOL).

BRAZIL. **Amazonas:** Município Jutai, Jutai (SW0266), *Daly et al.* 4179 (K, NY); Presidente Figueiredo, R. Uatuma, Represa de Balbina (SW0159), *Thomas et al.* 5362 (K, NY). **Pará:** Município Oriximina, R. Mapuera, Tres Ilhas (SW0157), *Cid Ferreira* 9693 (K).

19. *Guarea michel-moddeii* T.D.Penn. & S.A.Mori, *Brittonia* 45(3): 231, figs 1, 2 (1993). – Type: French Guiana, Saül, La Fumée Mountain trail, fl., *Mori, Gracie, Angell & Rothman* 20963 (holo NY; iso CAY, K). **Fig. 48E.**

Young shoots golden tomentose to villose at first, soon becoming glabrous and strongly suberous and fissured, 1–1.5 cm diam. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 8–17 cm long, semiterete to channelled on the upper surface, sparsely hirsute, rhachis 20–60 cm long, semiterete to channelled, sparsely hirsute; petiolule 3–7 mm long. *Leaflets* opposite, 3–10 pairs, 20–41 × 5–11 cm, oblong, apex obtuse, obtusely cuspidate to narrowly attenuate, base acute to obtuse, coriaceous, upper surface glabrous, lower surface with sparse hirsute indumentum on midrib and veins, sometimes glandular-punctate or -striate; venation eucamptodromous or brochidodromous in the upper half, midrib and secondary veins sunken on the upper surface, secondaries 15–18 pairs, ascending, straight or slightly arcuate, parallel or slightly convergent, intersecondaries short or absent, tertiaries oblique, all orders of venation strongly impressed on the upper surface and prominent below (bullate). *Inflorescence* cauliflorous, to 1 cm long, a few-flowered congested thyrse, sparsely pubescent, pedicel c.1 mm long. *Calyx* 2–3 mm long, cyathiform, irregularly 4-lobed, the lobes c.1.5 mm long, sparsely puberulous outside. *Petals* 4, valvate, c.1.3 cm long, c.3.5 mm broad, strap-shaped, apex acute, shortly appressed pubescent outside, glabrous inside, reflexing with age. *Staminal tube* c.9.5 mm long, c.4 mm broad, margin undulate, glabrous; anthers 8, c.1.5 mm long, glabrous. *Nectary* a broad stipe c.1 mm long, expanded to form a collar below the ovary, glabrous. *Ovary* 6–8-locular, locules with 2 superposed ovules, densely strigose, style glabrous, style-head discoid. *Capsule* 3–4 cm long, globose or depressed-globose, 6–8-valved, the valves with several anastomosing and convoluted fleshy ribs or wings up to 1 cm deep, sparsely hirsute, pericarp 2–4 mm thick (excluding the wings), valves with 2 superposed seeds. *Seeds* 1.3–1.5 cm long, c.1 cm broad, surrounded by a fleshy orange sarcotesta.

Field characters. Unbranched treelet to 5 m high, with deeply fissured and scaling suberous bark, with a large terminal cluster of spirally arranged strongly bullate leaves. The flowers are cream-coloured and the capsule bright red and covered with convoluted fleshy wings and ribs; the fruit is only tardily dehiscent. Flowering in September (only one collection seen) and mature fruit recorded in January, February, April, May and August.

Distribution and ecology. Known only from French Guiana and adjacent Brazil, where it occurs in the understorey on steep slopes and ridges in lowland rain forest up to 600 m altitude.

Collections examined. FRENCH GUIANA. Camp Caiman – Asarco – Mt. de Kaw (NW0452), *Bordenave & Raes* 5256 (CAY); Savane Roche de Virginie, bassin de l'Approuague (NW0452), *Cremers & Petronelli* 11868 (CAY, K); route Region – Saint Georges (NW0452), *Cremers & Gautier* 11959 (K, US); Montagne de Kaw (NW0452), *Delnatte* 1615 (CAY); 50 km SE of Saül (NW0354), *de Granville* 3505 (CAY); Station des Nouragues (NW0452), *de Granville et al.* 11170 (CAY, K, NY); Montagne Bellevue de l'Inini (NW0553), *de Granville et al.* 7749 (CAY, K); Mont Galbao (NW0353), *de Granville et al.* 8821 (CAY), *Pennington & Mori* 12100 (K), 12118 (CAY, K); Relais de Patawa (NW0452), *Mori et al.* 25352 (CAY); Montagne de Kaw (NW0452), *Oldeman* 2375 (CAY); Station des Nouragues (NW0452), *Prévost* 2211 (K); R. Arataye, 68 km SW of Regina, *Villiers* 4030 (CAY).

BRAZIL. **Amapá:** Município Macapá, Perimetral Norte (BR 210) (NW0153), *Daly et al.* 4027 (NY).

This species is morphologically close to *Guarea cristata* (western Amazonia). However, the very large and bullate subglabrous leaflets are very distinctive and unlike the smaller, non-bullate coarsely hirsute leaflets of *Guarea cristata*. There are also several quantitative floral and fruit differences between them, such as petals c.1.3 cm long in *Guarea michel-moddei* (versus 1.6–1.7 cm in *G. cristata*), and capsule 3–4 cm long and 6–8-valved in *G. michel-moddei* (versus capsule 4–6 cm long and 4–6-valved in *G. cristata*).

20. *Guarea subandina* W.Palacios, Fl. Ecuador 82, Fam. 98, Meliaceae: 44 (2007).

– Type: Ecuador, Zamora-Chinchipec, La Esmeralda, Cooperativa San Francisco de Numbala Alto, fl., *Palacios & Tirado* 13112 (holo QCNE; iso MO). **Figs 15, 53B.**

Young shoots pale tomentose, 7–8 mm diam., eventually becoming glabrous, pale whitish and slightly suberous. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 5–10 cm long, semiterete at the base to terete at the apex, tomentose at first, rhachis up to 50 cm long, slightly channelled above or terete, tomentose to pubescent; petiolule 6–10 mm long. *Leaflets* up to 5 pairs, 12–22 × 6–8 cm, elliptic or oblanceolate, apex acuminate to obtusely cuspidate, base acute to narrowly attenuate, thinly coriaceous, upper surface glabrous except for residual pubescence along the midrib, lower surface pale tomentose on midrib and veins, sparsely pubescent on the lamina, not glandular-punctate or -striate; venation eucamptodromous, midrib sunken on the upper surface, secondaries 16–18 pairs, ascending, parallel, slightly arcuate or straight, intersecondaries short or absent, tertiaries oblique, parallel. *Inflorescence* axillary, 15–20 cm long, racemose, tomentose. *Flowers* subtended by slender bracts 5–6 mm long; pedicel stout, 1–1.5 mm long. *Calyx* cyathiform, c.5 mm long, with 4 shallow broadly ovate, obtuse lobes, pubescent outside, subglabrous inside. *Petals* 4, valvate, free, 16–17 mm long, 3–4 mm broad, strap-shaped, apex acute, sericeous outside, glabrous inside. *Staminal tube* 10–12 mm long, 4–5 mm broad, margin undulate, glabrous; anthers

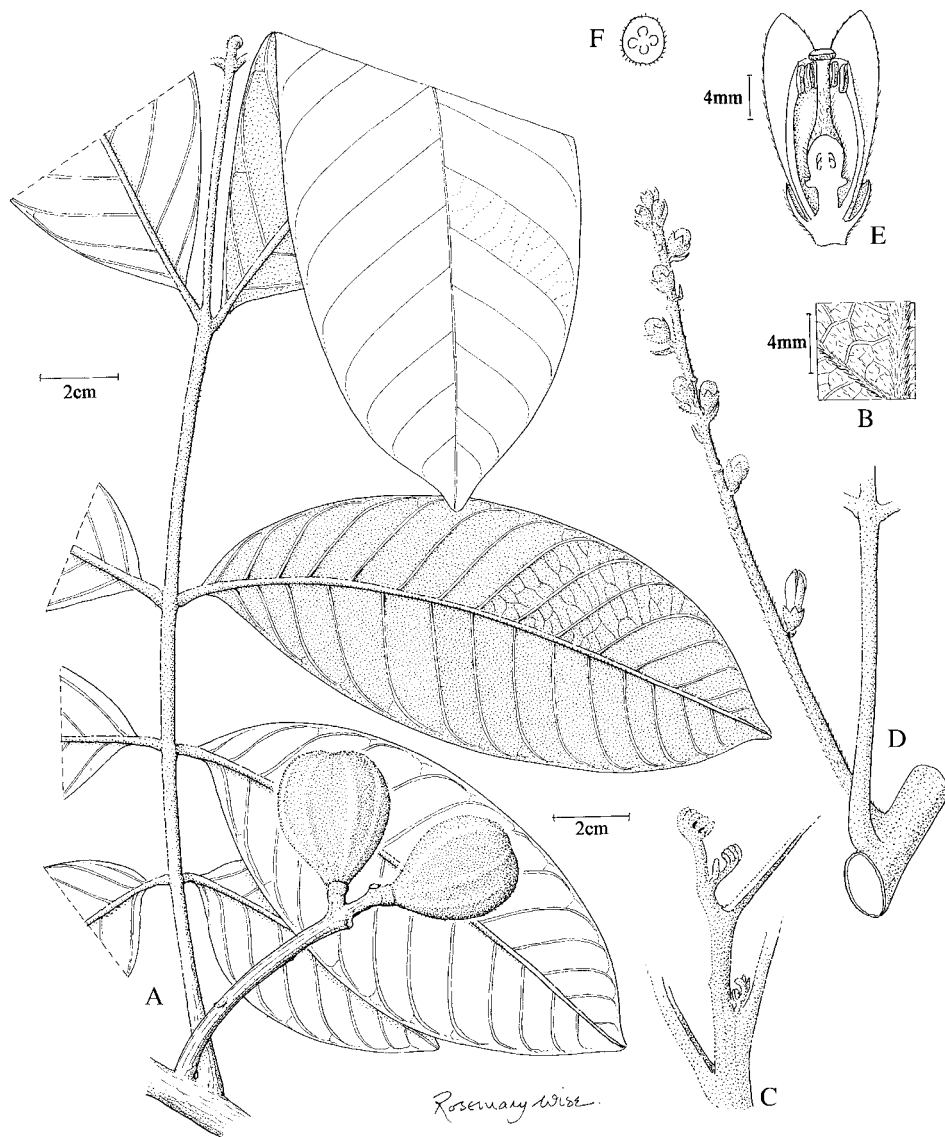


FIG. 15. *Guarea subandina* W. Palacios. A, habit with fruit; B, enlargement of leaf undersurface; C, shoot apex; D, young inflorescence; E, half-flower; F, cross-section of ovary. (A-C, E, F, *Chimbo & Chamba* 34; D, *Diaz & Torres* 7780).

8, 1.5–1.7 mm long, oblong, glabrous. *Nectary* a stout stipe c.2 mm long, expanded below the ovary, glabrous. *Ovary* 4-locular, locules with 2 superposed ovules, densely tomentose, style c.6 mm long, tomentose below, glabrous at the apex, style-head discoid. *Capsule* (immature) 3–4 cm long, 3–3.5 cm broad, obovoid, apex rounded or truncate, base acute, 4-valved, valves with 2 superposed seeds, valves

± smooth, velutinous mixed with sparser, longer hairs, slightly longitudinally ribbed when dry, pericarp c.5 mm thick. *Seed* immature.

Field characters. Tree to 20 m high and 25 cm diam. with whitish flowers and dark reddish brown fruit. Flowering recorded in October and May, immature fruit in May.

Distribution and ecology. Southern Ecuador and northern Peru in wet montane and cloud forest between 2000 m and 2400 m altitude.

Collections examined. ECUADOR. **Loja:** Estación Científica San Francisco (SW0379), *Alvarez et al.* 2809 (NY). **Loja-Zamora-Chinchipe:** km 30 Loja-Zamora, Estación Científica San Francisco (SW0379), *Chimbo & Chamba* 34 (K, QCNE), 110 (MO, QCNE), *Neill et al.* 12696 (K). **Zamora-Chinchipe:** new road Loja-Zamora, Quebrada del Diablo (SW0379), *van der Werff & Palacios* 9233 (K).

PERU. **Cajamarca:** San Ignacio Province, Sr. José de Lourdes (SW0578), *Diaz & Torres* 7780 (QCNE).

Guarea subandina is morphologically close to *G. carinata* (lowland Amazonia). They are similar in leaf morphology, indumentum and floral size and structure. The main differences lie in the inflorescence structure (slender raceme 15–20 cm long, probably with indeterminate apical growth versus a short panicle 2–10 cm long in *Guarea carinata*) and in the fruit structure (smooth versus prominently ribbed in *G. carinata*). *Guarea subandina* occurs in high montane and cloud forest over 2000 m altitude, whereas *G. carinata* is confined to lowland and lower montane forest.

21. *Guarea pubescens* (Rich.) A.Juss., Bull. Sci. Nat. Géol. 23: 240 (1830); Mém. Mus. Hist. Nat. 19: 241, 286 (1831); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 293 (1981). – *Trichilia pubescens* Rich., Actes Soc. Hist. Nat. Paris 1: 108 (1792). – Type: Cayenne (French Guiana), fl., *Leblond* 61 (holo G; iso P (fragment)).

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 295–296 (1981).

Abbreviated description. Indumentum of young shoots and inflorescences coarsely pubescent, leaves with indeterminate apical growth, leaflets 2–7 pairs, 9–26 × 2.8–10(–12) cm, elliptic, oblong, oblanceolate or lanceolate, lower surface pubescent or glabrous, secondary veins 8–12(–15) pairs, tertiary veins oblique, usually numerous, straight and closely parallel, inflorescence 2–15(–30) cm long, a few-flowered slender raceme or thyrses, petals (3–)4(–5), valvate, 7–9(–12) mm long, staminal tube 5–7(–9) mm long, 1.5–3 mm broad, anthers (7–)8(–9), ovary 4(–5)-locular, locules 1-ovulate, densely long-strigose, capsule 1.2–2 cm long, depressed globose or globose, 4-valved, valves obscurely 3(–4)-ribbed and often minutely tuberculate between the ribs, pericarp 0.5–1.5(–2) mm thick, puberulous intermixed with coarser hairs, valves 1-seeded.

Key to the subspecies of Guarea pubescens

- 1a. Leaves usually broadly elliptic or oblanceolate, often less than 3 times as long as broad, midrib usually sunken and slightly puberulous, upper lamina with minute raised dots, petiole and rhachis unwinged, capsule often globose and minutely tuberculate, ribbed or not _____ **21a.** subsp. **pubescens**
- 1b. Leaves narrowly elliptic or lanceolate, usually more than 3 times as long as broad, midrib raised on the upper surface, glabrous, upper lamina without raised dots, petiole and rhachis narrowly winged, capsule depressed globose, irregularly ribbed _____ **21b.** subsp. **pubiflora**

21a. *Guarea pubescens* subsp. *pubescens*. Figs 16, 48F.

Distribution and ecology. Venezuela and the Guianas, northern and central Amazonian Brazil, Amazonian Colombia, Ecuador, Peru and Bolivia, occurring in non-flooded lowland rain forest.

Representative additional collections. COLOMBIA. **Amazonas:** R. Caqueta, El Engano (SW0071), *Duivenvoorden et al.* 1574 (K). **Caqueta:** Araracuara (SW0072), *Gentry & Sanchez* 65007 (K).

VENEZUELA. **Amazonas:** Atabapo, Rio Padamo (NW0365), *Marin* 839 (K). **Apure:** Pedro Camejo, Fundo Las Delicias (NW0768), *Gomez & Bevilacqua* 320 (K). **Bolívar:** Municipio Sucre, Helipuerto 23 (NW0664), *Delgado* 1014 (K). **Zulia:** 55 km SW of Machiques, Aricuaia (NW0972), *Liesner & Gonzalez* 13143 (K).

GUYANA. Upper Takutu-Upper Essequibo, Kwitaro River (NW0358), *D. Clarke et al.* 6515 (K); Potaro-Siparuni region, Iwokrama Reserve (NW0458), *Mutchnick* 946 (K).

SURINAM. Sipaliwini, along Ulemari River, 13 km upstream from confluence with Litani River, (NW0354), *Hammel et al.* 21298 (K).

FRENCH GUIANA. Haut Litany-Bassin de Litany (NW0254), *de Granville et al.* 11962 (K).

ECUADOR. **Morona-Santiago:** Taisha (SW0277), *Little et al.* 747 (COL, QCNE). **Orellana:** Rio Tiputini, Yasuní Scientific Research Station (SW0076), *Bass* 357 (F, NY). **Sucumbíos:** Cantón Lago Agrio, Dureno (SW0076), *Cerón* 378 (NY).

PERU. **Amazonas:** Condorcanqui, El Cenepa, Mamayaque (SW0478), *Vásquez et al.* 22284 (F). **Loreto:** Iquitos, Puerto Almendras (SW0373), *Pennington et al.* 12467 (K, MOL). **Madre de Dios:** Tambopata Explorer's Inn Tourist Camp (SW1269), *Gentry et al.* 51439 (K). **Ucayali:** Von Humboldt Reserve (SW0875), *Pennington et al.* 16514 (K, MOL).

BRAZIL. **Acre:** Feijo, basin of R. Muru (SW0871), *Delprete et al.* 8517 (K). **Amapá:** Reserva INCRA Rio Falsino (NW0151), *Campbell et al.* 14472 (K). **Pará:** Ilha de Marajó, Rio Jipuru (SW0050), *Tavares* 233 (K).

BOLIVIA. **Pando:** Nicolas Suarez, Campamento San Sebastian (SW1169), *Paniagua et al.* 2018 (F, K).

21b. *Guarea pubescens* subsp. *pubiflora* (A.Juss.) T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 298 (1981). – *Guarea pubiflora* A.Juss., Bull. Sci. Nat. Géol. 23: 240 (1830); Mém. Mus. Hist. Nat. 19: 241, 287 (1831). – Type: Brazil, Amazonas (Rio Negro), Barcellos, fl., *Collector unknown* s.n. (holo P). Figs 16, 49A.

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 298 (1981).

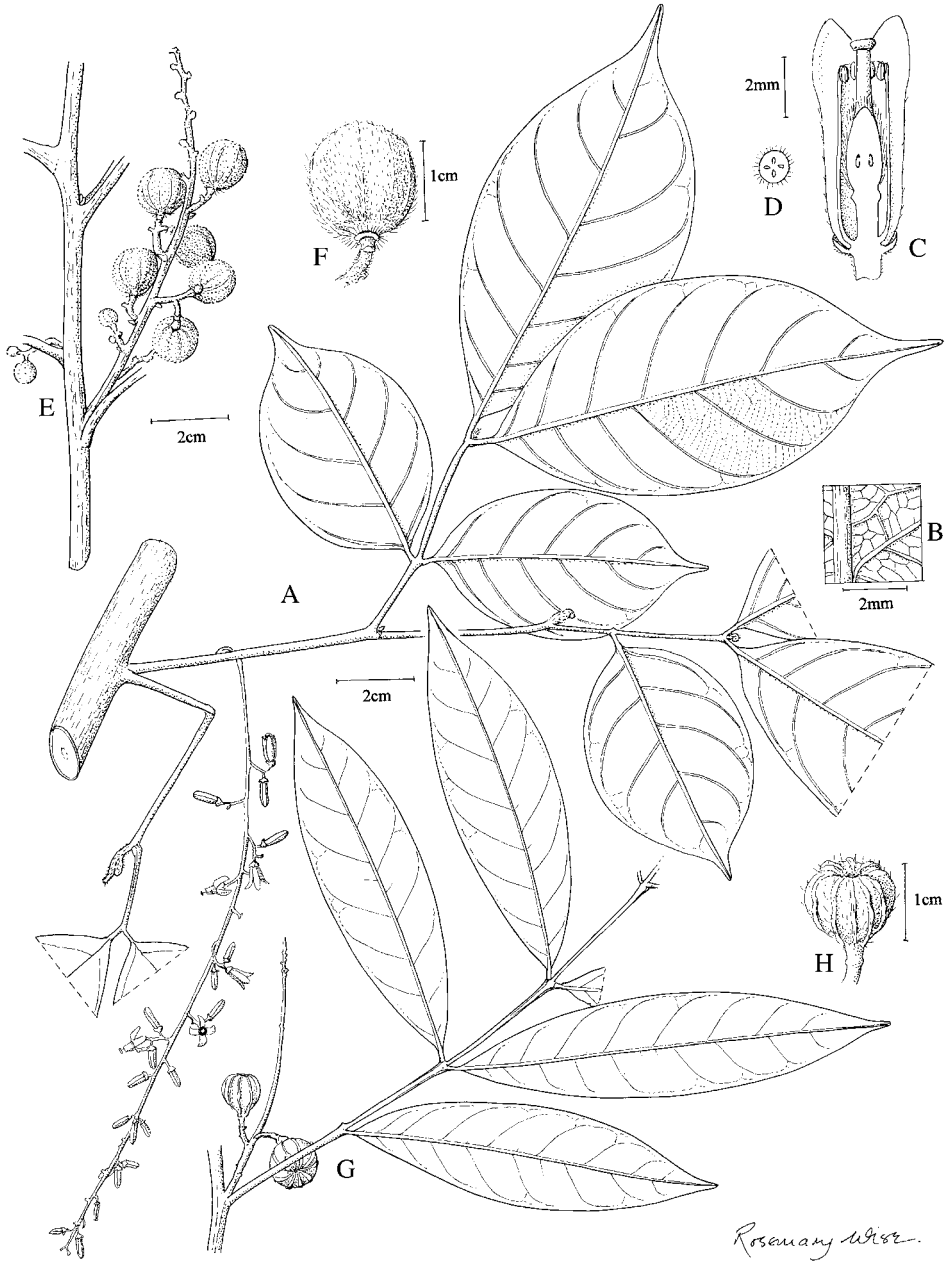


FIG. 16. *Guarea pubescens* (Rich.) A.Juss. A–F, subsp. *pubescens*: A, habit; B, enlargement of leaf undersurface; C, half-flower; D, cross-section of ovary; E, infructescence; F, fruit. G, H, subsp. *pubiflora* (A.Juss.) T.D.Penn.: G, habit; H, fruit. (A–D, Mori & Pipoly 15626; E, F, Jenman 316; G, H, Acevedo-Rodriguez et al. 7967).

Distribution and ecology. Southern Venezuela, French Guiana and central and southern Amazonian Brazil, confined to riverbanks and periodically and permanently flooded forest. Common along the middle reaches of the Amazon river and along its major tributaries, but apparently not reaching Peru or Ecuador. In Venezuela it is common along the middle and upper Orinoco basin. We have seen no records yet from Colombia, but it is almost certainly to be found along the rivers which share a frontier with Venezuela.

Representative additional collections. VENEZUELA. **Apuré:** Distrito Romulo Gallegos, between Laguna del Término and Rio Capanaparo (NW0669), *Davidse & Gonzalez* 16158 (K).

FRENCH GUIANA. Le Tampoc, above Saut Koumaiou Soula (NW0353), *Cremers* 4505 (K); Bas-Camopi (NW0352), *Oldeman* 1330 (K).

BRAZIL. **Amazonas:** R. Parauari, tributary of R. Maues-Acu, at Agua Mineral (SW0457), *Hill et al.* 13073 (K).

BOLIVIA. **La Paz:** Prov. Iturralde, Luisita (SW1367), *Beck & Haase* 10162 (K). **Pando:** Prov. Federico Roman, Rio Abuna (SW0965), *Vargas et al.* 1049 (K). **Santa Cruz:** Prov. Velasco, El Refugio Ecological Reserve (SW1461), *Guillen & Chore* 3379 (K).

22. *Guarea zarcerensis* Coronado, *Novon* 16(4): 466 (2006). – Type: Costa Rica, Alajuela, San Carlos, Sucre [NW1084], fl., *A. Smith* 1686 (holo NY; iso F, MO). **Figs 17, 59B.**

Young shoots 3–4 mm diam., pale-pubescent at first, soon glabrous, pale buff, smooth, with or without large pustular lenticels. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 5–9 cm long, semiterete to slightly channelled at the base, glabrous, rhachis 8–18 cm long, semiterete, glabrous; petiolule 1.5–1.7 cm long. *Leaflets* 3–6 pairs, 9.5–18.5 × 4–8.6 cm, broadly elliptic, apex obtusely cuspidate, base narrowly attenuate and decurrent on the petiolule, chartaceous, glabrous, obscurely glandular-striate; venation eucamptodromous, midrib flat on the upper surface (not raised or sunken), secondaries 5–7 pairs, ascending, slightly arcuate and convergent, intersecondaries few, moderate to long, or absent, tertiaries oblique, obscure. *Inflorescence* axillary and on twigs below the leaves, 4–15 cm long, a slender lax-flowered panicle, the lower lateral branches to 1–1.5 cm long, with scattered minute appressed hairs or glabrous; pedicel 3–4 mm long, with sparse appressed hairs. *Calyx* closed in bud, in male flower 2.5–3.5 mm long, cup-shaped and irregularly 3–4-lobed to c.1/2 its length, with scattered minute appressed hairs outside, glabrous inside. *Petals* 4, 6–8 × 2–3 mm, strap-shaped, apex acute, appressed puberulous outside, glabrous inside. *Staminal tube* 5–6 × 2–2.5 mm, cylindrical, margin undulate, glabrous; anthers 8–9, c.1.5 mm long, glabrous. *Nectary* a short stout stipe below the ovary. *Ovary* ovoid, c.2 mm long, 4–6-locular, locules with 1–2 superposed ovules, appressed pubescent, style c.2 mm long, style-head discoid. Female flowers not seen. *Capsule* c.2.5 × 3 cm, depressed-globose, apex truncate, base obtuse, 4–6-valved, valves strongly and irregularly ribbed, the ribs anastomosing and strongly tuberculate in the upper half, minutely puberulous, pericarp 3–5 mm thick, valves with 1–2 superposed seeds. *Seed* (immature), 6–8 mm long.



FIG. 17. *Guarea zarceroensis* Coronado. A, habit; B, half-flower; C, fruit. (A, B, *Smith, A.* 1686; C, *Smith, A.* 2899).

Field characters. Tree to 30 m high and 1 m diam., but flowering when a small treelet 2–3 m high, bark brown and scaling. Flowers with white or cream-coloured petals and yellow anthers. Capsule hard and strongly tuberculate. Flowering recorded in March, July and October, with a single fruiting collection in July.

Distribution and ecology. Known only from Alajuela and Limón, Costa Rica, in wet lowland and montane rain forest between 500 m and 1550 m altitude.

Collections examined. COSTA RICA. **Alajuela:** Upala, PN Rincon de la Vieja, Cuenca del Pizote (NW1085), Gonzalez & Porras 3911 (INB); Upala, Dos Rios, 5 km S of Brasilia (NW1085), Herrera 1053 (K, MO); San Luis de Zarcero (NW1084), A. Smith 861 (F, MO); Alfaro Ruiz, Zarcero (NW1084), A. Smith 2899 (F). **Limón:** Matina, RI Barbila-Dantas, Cuenca de Matina (NW1083), Rodríguez *et al.* 6121 (INB).

In the absence of fruits, specimens belonging to this species were wrongly assigned to *Guarea glabra* in the *Flora Neotropica* treatment (Pennington *et al.*, 1981). It is distinctive in its combination of few secondary veins (5–7 pairs), leaflets with long petiolules, flowers on long pedicels and 4-merous flowers with pubescent petals and ovary. Its strongly ribbed and tuberculate fruit is similar to that of the South American *Guarea macrophylla* but the few secondary veins, long petiolule, long pedicel and lax-flowered inflorescence are distinctive.

The ITS phylogeny indicates a relationship that is not supported by the morphology, with *Guarea zarceroensis* placed in a small group containing *G. tafae-malekui* and *G. macrocalyx*, and all apparently having arisen recently from South American stock.

23. *Guarea tafae-malekui* Al.Rodr., Lankesteriana 6: 115 (2006). – Type: Costa Rica, Alajuela, San Carlos, Parque Nacional Arenal, basin of San Carlos, Cerro Chato, fl., fr., A. Rodríguez *et al.* 6238 (holo INB; iso CR, MO). **Figs 18, 59C.**

Young shoots 1.2–1.5 cm diam., hollow, minutely puberulous at first, soon glabrous, pale brown, smooth, without lenticels. *Leaves* pinnate with a terminal bud with intermittent growth, petiole 10–28 cm long, channelled at the base to semiterete at the apex, minutely puberulous to glabrous, rhachis up to 55 cm long, semiterete, subglabrous; petiolule 5–7 mm long, glabrous. *Leaflets* opposite, up to 8 pairs, 17–32 × 6–10 cm, broadly oblong or oblanceolate, apex narrowly attenuate, base acute or narrowly cuneate, chartaceous, glabrous, not glandular-punctate or -striate; venation eucamptodromous, midrib flat or slightly sunken on the upper surface, secondaries 13–15 pairs, ascending, slightly arcuate, slightly convergent, intersecondaries absent, tertiaries numerous, fine, oblique. *Inflorescence* axillary or below the leaves, 8–15 cm long, a slender, few-flowered panicle, lateral branches to 3 cm long; pedicel up to 5 mm long, with 3–4 bracteoles 3–10 mm long. Male flowers only seen. *Flowers* subtended by bracts 4–6 mm long, narrowly lanceolate, keeled. *Calyx* 7–10 mm long, cup-shaped with 4 shallow to deep lobes, lobes ovate, slightly keeled, abruptly contracted at the apex into an acumen 1–2 mm long, densely puberulous. *Corolla* acute in bud, petals 4, 1.5–1.7 cm long, 8–10 mm broad, apex acute,

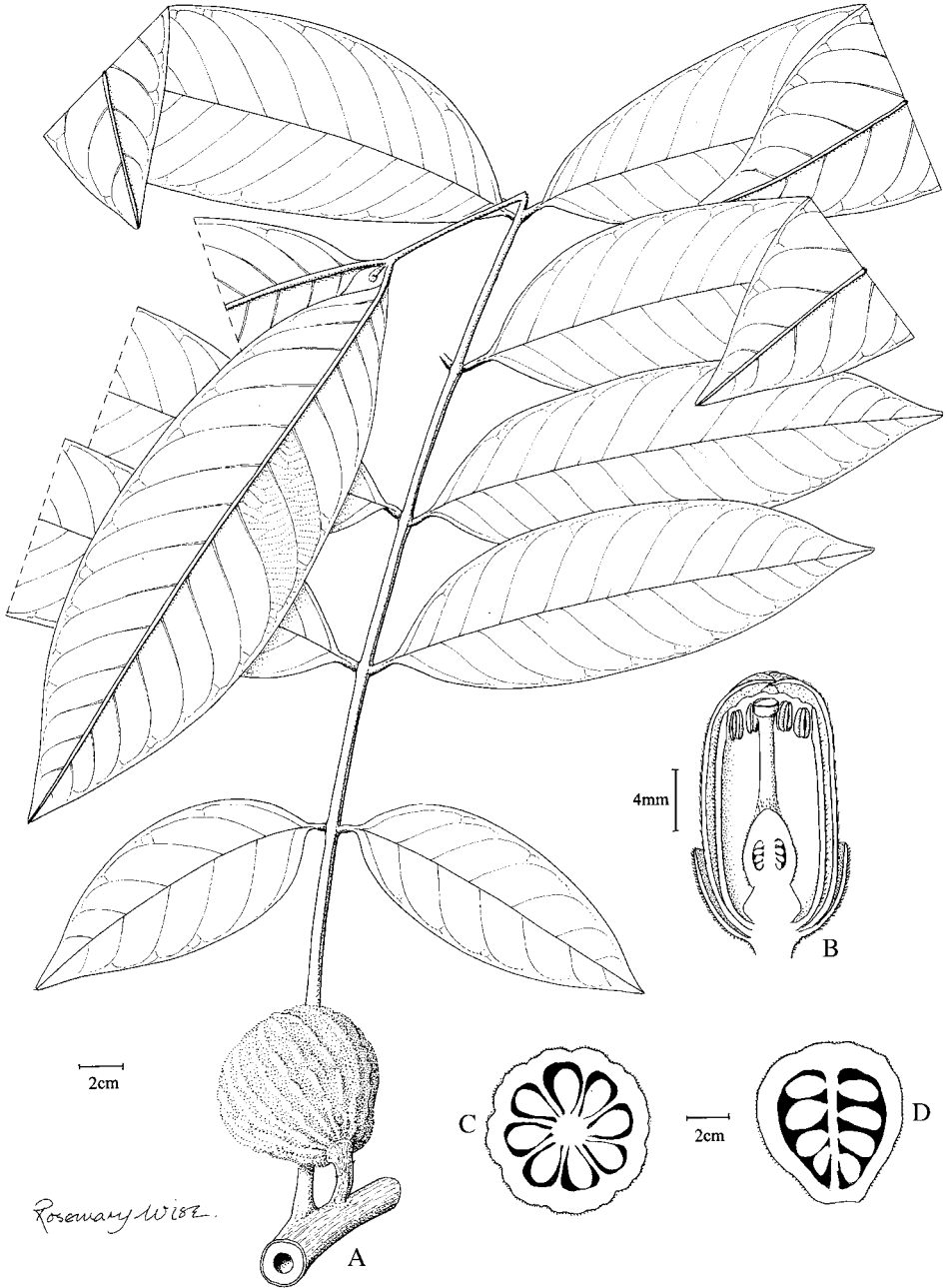


FIG. 18. *Guarea tafae-malekui* Al.Rodr. A, habit with fruit; B, half-flower; C, cross-section of fruit; D, longitudinal section of fruit. (A, C, D, *Funk et al.* 10772; B, *Rodriguez et al.* 6238).

sericeous outside, papillose inside. *Staminal tube* 1.4–1.6 cm long, 7–9 mm broad, margin denticulate, papillose outside; anthers 8–9, c.3 mm long, glabrous. *Nectary* 2–2.5 mm long, a stout stipe expanded below the ovary, glabrous. *Ovary* 6–8-locular, locules with (3–)4 superposed ovules, minutely sericeous. *Capsule* c.6 × 7 cm, globose to broadly pyriform, apex obtuse to truncate, base obtuse, finely puberulous, 6–8-valved, pericarp c.1 cm thick, slightly tuberculate and ribbed when dry, valves 1–4-seeded. *Seeds* 0.5–1.6 cm long, surrounded by a thin sarcotesta.

Field characters. Monopodial treelet to 5 m high, flowers creamy white, mature fruit reddish brown. Flowering and fruiting recorded in February.

Distribution and ecology. Costa Rica, in wet forest on the Caribbean slopes of the Cordillera de Tilarán, between 400 m and 1000 m altitude.

Collections examined. COSTA RICA. **Alajuela:** Arenal Volcano, Macadamia field to river (NW1084), *Funk et al.* 10772 (MO, US); San Carlos, Volcan Arenal, Fortuna, track to Tabacón (NW1084), *Jiménez et al.* 1458 (INB), *Rodríguez* 8526 (INB); San Carlos, La Fortuna, R.B. Arenal (NW1084), *Rodríguez & Lepiz* 9949 (INB), 9950 (INB), 9951 (INB), 9952 (INB), 9953 (INB). **Guacacaste:** 6 km N of Rio Chiquito, above Lake Arenal (NW1084), *Haber et al.* 4825 (CR).

This is an interesting and morphologically very distinct species. The multilocular ovary with 3–4 ovules in each locule is unique to the subfamily Melioideae. Hitherto, multiovulate ovary locules have been known only in species of subfamily Cedreloideae. Other unusual characters are the calyx lobes with a sharp apical acumen and the acute corolla, unlike any other *Guarea* except *G. macrocalyx*. The species is easily recognised by the hollow twigs, large leaflets, large flowers, acuminate calyx lobes, large (1.5–1.7 cm long) acute corolla (when in bud), 6–8-locular ovary with 3–4 ovules in each locule, and large multilocular capsule with several seeds in each valve. The ITS phylogeny places this species next to *Guarea macrocalyx*.

24. *Guarea macrocalyx* Al.Rodr., Lankesteriana 6: 110 (2006). – Type: Costa Rica, San José, Perez Zelendon, Tinamaste, Finca de los Suizos, fl., *A. Estrada* 832 (holo CR; iso INB). **Figs 19, 59D.**

Young shoots 6–9 mm diam., not hollow, minutely puberulous at first, soon becoming glabrous, smooth, pale buff, with scattered lenticels. *Leaves* pinnate with a terminal bud with intermittent growth, petiole 10–20 cm long, semiterete, puberulous to glabrous, rhachis up to 50 cm long, semiterete, glabrous; petiolule 1–1.6 cm long. *Leaflets* opposite, up to 7 pairs, 17.5–33 × 8.4–13.5 cm, elliptic to broadly lanceolate, apex acuminate to obtusely cuspidate, base acute, obtuse or rounded, chartaceous, glabrous, not glandular-punctate or -striate; venation eucampitodromous, midrib flat or slightly raised (rounded) on the upper surface, secondaries 12–16 pairs, ascending, straight or slightly arcuate, mostly parallel, intersecondaries absent, tertiaries numerous, fine, oblique. *Inflorescence* axillary or ramiflorous, 5–25 cm long, a slender raceme or panicle, few- to many-flowered, lateral branches to

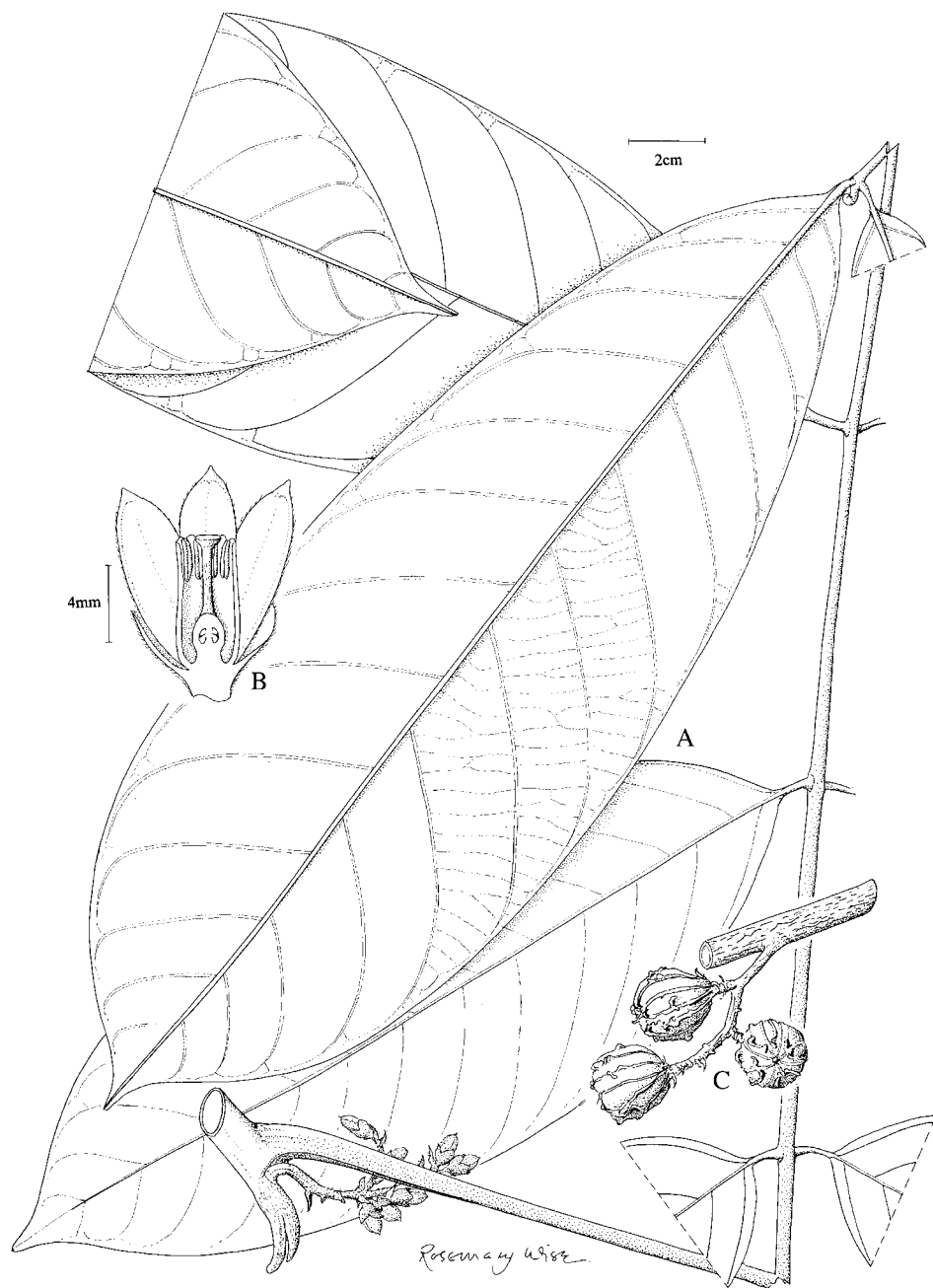


FIG. 19. *Guarea macrocalyx* Al.Rodr. A, habit; B, half-flower; C, fruit. (A, B, Herrera *et al.* 7392; C, Kernan 1214).

5 cm long, finely puberulous; pedicel 2–4 mm long, bracteoles 4–5 mm long, subulate. *Flower buds* oblong, narrowly acute at the apex. *Flowers* subtended by sharply acute lanceolate bracts, c.5 mm long. *Calyx* closed in bud, 5–14 mm long, cyathiform, 2–3-lobed to halfway or more, lobes keeled, contracted at the apex into a slender subulate point, sparsely puberulous, calyx usually persists in fruit. *Corolla* apex acute in bud, petals 4–6, 8–14 cm long, 3.5–5 mm broad, apex acute, sericeous outside, papillose inside. *Staminal tube* 6–9 mm long, c.3 mm broad, margin crenulate, glabrous; anthers 8–9, 1.75–2.5 mm long, glabrous. *Nectary* a broad stipe c.1 mm long. *Ovary* 1.5–1.75 mm long, 4–5-locular, locules with 2 superposed ovules, densely pubescent, style 5–6 mm long, style-head discoid. *Capsule* (immature) c.2 × 2 cm, ± globose or broadly pyriform, apex truncate, base obtuse, 4–5-valved, valves with 1–2 superposed seeds, each valve with 3 shallow longitudinal ribs, the ribs tuberculate in the upper half, finely puberulous intermixed with longer hairs, pericarp c.1 mm thick. *Seeds* not seen.

Field characters. Unbranched treelet to 3.5 m high with whitish flowers, flowering in December and January, fruit maturing in August.

Distribution and ecology. Costa Rica, in rain forest on both the Pacific and Caribbean slopes (Limón and Puntarenas), and in the Osa Peninsula, up to 900 m altitude.

Collections examined. COSTA RICA. **Limón:** Talamanca, Cuenca de Sixaola, San Miguel, (NW0982), *Gonzalez* 1711 (INB). **Puntarenas:** Osa, Reserva Forestal Golfo Dulce, Aguabuena (NW0883), *Aguilar* 790 (INB); Cantón de Golfito Jimenez, Dos Brazos del Rio Tigre, Cerro Rincón (NW0883), *Herrera* 4162 (INB, K); Cantón de Osa Sierpe, San Juan, between Guerra and San Juan, track to Cerros Chocuaco (NW0883), *Herrera* 4876 (INB, MO); Corcovado National Park, Sirena, Los Patos (NW0883), *Kernan* 1214 (INB, K).

The calyx of this species is unusual but similar to that of *Guarea tafae-malekui*: deeply 2–3-lobed, the lobes keeled and contracted at the apex into a subulate point, and it is usually persistent in fruit. The acute corolla bud is also unusual and the small ribbed and tuberculate capsule is distinctive.

Only the type specimen has large flowers and the fruit seen by us are only half the size of that in the protologue.

25. *Guarea velutina* A.Juss., Bull. Sci. Nat. Géol. 23: 240 (1830); A.Juss., Mém. Mus. Hist. Nat. 19: 241, 288 (1831); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 299, fig. 60 (1981). – Type: Brazil, fl., *Collector unknown*, annotated ‘Herbar Lusitanicum, Bresil’ (holo P). **Fig. 49B.**

Abbreviated description. Young shoots velutinous to tomentose, leaves with indeterminate apical growth, leaflets 2–6 pairs, 10–21 × 4.6–7.3 cm, elliptic, oblong or lanceolate, base usually obtuse or truncate, coriaceous, lower surface densely pubescent with crisped hairs to subglabrous, and with minute red papillae, tertiary veins obscure, inflorescence 4–33 cm long, a pyramidal thyse, petals 3–5, valvate, 7–10 mm long, 1.5–2.5 mm broad, staminal tube 6–8 mm long, 2–2.5 mm broad,

anthers 8–9, ovary ribbed, 4–5-locular, locules 1-ovulate, densely pubescent, capsule c.3.5 cm long, 3.5–4.5 cm broad, 4-valved, \pm globose, each valve with 3–4 thin convoluted and anastomosing longitudinal wings up to 1 cm deep, finely puberulous, pericarp (excluding wings), 3–5 mm thick, valves 1-seeded.

Distribution and ecology. Amazonian Colombia, Guyana and Amazonian Brazil, a plant of lowland rain forest on non-flooded sites, sometimes recorded from poorly drained land.

Additional collections examined. COLOMBIA. **Amazonas:** R. Caqueta, by Isla Sumaeta (SW0072), *van Dulmen* 372 (K).

GUYANA. Region Upper Takutu-Upper Essequibo, Kuyuwini R., Honey Creek (NW0159), *D. Clarke* 4461 (K), 4594 (K); South Kassikaityn R., to Wassarai Mts. (NW0159), *D. Clarke et al.* 7932 (K), 8056 (K).

BRAZIL. **Acre:** Upper R o Moa near Fazenda Arizona (SW0773), *Campbell et al.* 6523 (K); Municipio Novo Airao, Rio Camanau, Aldeia Mar  (SW0161), *Milliken et al.* (*Miller* 345) (K). **Amazonas:** western massif of Serra Araca (NW0063), *Prance et al.* 29462 (K); Manaus, Distrito Agropecuario, BR 174, km 72 (SW0260), *da Silva et al.*, INPA/WWF 2108.412.2 (K); Presidente Figueiredo, Represa de Balbina (SW0159), *Thomas et al.* 5306 (K). **Par :** Municipio Oriximina, BR 163, 14 km N of Cachoeira Porteira (SW0057), *Cid Ferreira et al.* 7945 (F, K). **Rondonia:** Municipio de Porto Velho, Reservatorio de Usina Hidreletrica de Samuel (SW0863), *Cid Ferreira et al.* 7546 (K).

This species is morphologically close to *Guarea juglandiformis*, but no ITS sequence data were available to confirm whether they are related.

26. *Guarea costata* A.Juss., Bull. Sci. Nat. G ol. 23: 240 (1830); A.Juss., M m. Mus.

Hist. Nat. 19: 241, 291 (1831); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 303, fig. 61 (1981). – Type: Cayenne (French Guiana), young fr., *Perrottet* s.n. (holo P).

Figs 20, 49C.

Abbreviated description. Young shoots and inflorescences finely appressed puberulous, leaves with a terminal bud showing intermittent growth, leaflets up to 6 pairs, 13–20 \times 5–6.6 cm, usually oblanceolate, or broadly oblong, subcoriaceous, glabrous, secondary veins 8–11 pairs, inflorescence axillary, 6–12 cm long, a slender thyrs, petals 4, valvate, 5.5–6.5 mm long, staminal tube 5–5.5 mm long, 1.5–2 mm broad, anthers 8, ovary 4-locular, locules 1-ovulate, capsule c.2 cm long (including the stipe), c.1.8 cm broad, globose or depressed globose, contracted at the base into a stipe 0.5–0.8 cm long, 4-valved, each valve with 3 longitudinal ribs or narrow wings to 2.5 mm deep, pericarp c.2 mm thick, minutely appressed puberulous, with minute red papillae, valves 1-seeded.

Distribution and ecology. Surinam and French Guiana, in lowland rain forest on non-flooded lateritic sites.

Additional collections examined. SURINAM. Lely Mountains, SW plateau (NW0454), *Lindeman et al.* 97 (U), 130 (K, NY), 236 (K).

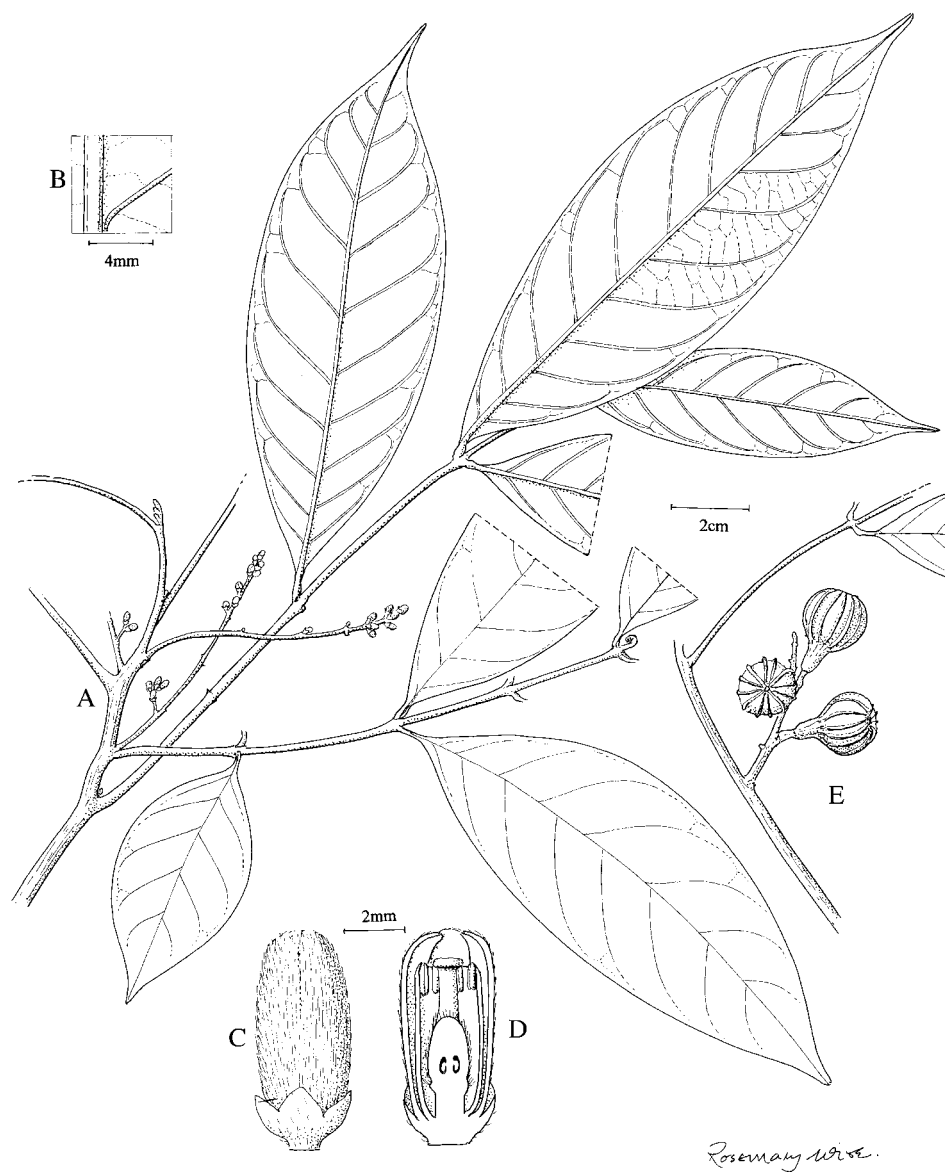


FIG. 20. *Guarea costata* A.Juss. A, habit; B, enlargement of leaf undersurface; C, flower bud; D, half-flower; E, infructescence. (A, C, D, Lindeman et al. 130; B, Amshoff 2500; E, de Granville 8072).

FRENCH GUIANA. Montagne Bellevue de l'Inini (NW0353), de Granville et al. 8072 (K, U); Mont Atachi Bacca (NW0353), de Granville et al. 10707 (K); Bassin de Sinnamary, Crique Plomb (NW0553), Loubry 1729 (K).

Closely related to *Guarea velutina* which also shares the winged capsule.

- 27. *Guarea guentheri*** Harms, Notizbl. Bot. Gart. Berlin-Dahlem 10: 243 (1928); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 352 (1981). – Type: Peru, Amazonas, mouth of R. Santiago, fl., *Tessmann* 4156 (holo B, destroyed; lecto NY, designated here; isolecto F (fragment)). **Figs 21, 53C.**

Abbreviated description. Young shoots and inflorescences appressed puberulous to shortly pubescent, leaves with a terminal bud showing intermittent growth, leaflets up to 6 pairs, 18–31 × 7–11 cm, elliptic, oblong or oblanceolate, chartaceous, ± glabrous above, sparsely pubescent on midrib and veins below, and lamina with numerous minute red papillae, secondary veins 14–18 pairs, inflorescence axillary, ramiflorous or cauliflorous, 5–20 cm long, a slender panicle, sometimes with several branches from the base, petals 4, valvate, 12–15 mm long, densely appressed puberulous outside, staminal tube 9.5–12 mm long, 2.5–3 mm broad, anthers (7–)8, ovary 4-locular, locules with 2 superposed ovules, capsule 4–6.5 × 2.2–3 cm, shortly botuliform to ± pyriform, sometimes slightly constricted between the seeds, tapering at the base into a stout stipe c.1 cm long, obscurely ribbed, ribs plicate or torulose, minutely puberulous, 4-valved, valves with 2 superposed seeds, pericarp 2–5 mm thick.

Distribution and ecology. Extreme western Amazonian Brazil, Amazonian Ecuador and Peru, ascending to 900 m altitude in the foothills of the Andes. It is a small tree of rain forest on non-flooded sites.

Additional collections examined. ECUADOR. **Morona-Santiago:** Cordillera de Cutucú, Centro Shuar (SW0277), *Toasa & Tirado* 8731 (MO). **Napo:** 8 km below Misahuallí, Jatun Sacha Reserve (SW0177), *Palacios & Neill* 957 (K, MO). **Orellana:** Estación Experimental INIAP Napo, Payamino (SW0077), *Palacios et al.* 1180 (MO); Estación Experimental INIAP, San Carlos (SW0076), *Palacios & Neill* 1272 (K). **Pastaza:** Villano-Triunfo km 17 (SW0177), *Palacios* 12097 (K). **Sucumbios:** Lumbaqui (NW0077), *Pennington et al.* 12229 (K).

PERU. **Amazonas:** Bagua Province, Yamayakat (SW0478), *Jaramillo et al.* 1080 (K), 1186 (MO); Imaza, Kampanensa (SW0478), *Rodriguez* 618 (K); Rio Santiago, Caterpiza (SW0377), *Tunqui* 333 (MO). **Loreto:** Yanamono, Explorama Tourist Camp (SW0372), *Gentry et al.* 60908 (K, MO); Napo District, Rio Santa Maria (SW0174), *King* 506 (K); Maynas, Iquitos, R. Itaya, Buena Suerte (SW0373), *Vásquez & Jaramillo* 8433 (MO). **Pasco:** Oxapampa, Pichis valley, near Paujil (SW1074), *Foster et al.* 8932 (F, K).

BRAZIL. **Acre:** upper Rio Moa, near Fazenda Arizona (SW0773), *Campbell et al.* 6443 (K).

The dried leaves and fruit smell strongly of curry powder. It is the only species of *Guarea* recognisable by smell alone.

- 28. *Guarea macrophylla*** Vahl, Eclog. Amer. 3: 8 (1807); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 281, fig. 57 (1981). – Type: St. Croix, Montserrat, fl., *Ryan* s.n. (holo C). **Figs 22, 23.**

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 282 (1981).

Abbreviated description. Indumentum inconspicuous, puberulous or pubescent, leaves with indeterminate apical growth or not, leaflets 2–7(–9) pairs, 6–25(–33) × 2.6–8(–10.5) cm, elliptic, oblong or oblanceolate, rarely obovate, secondary veins

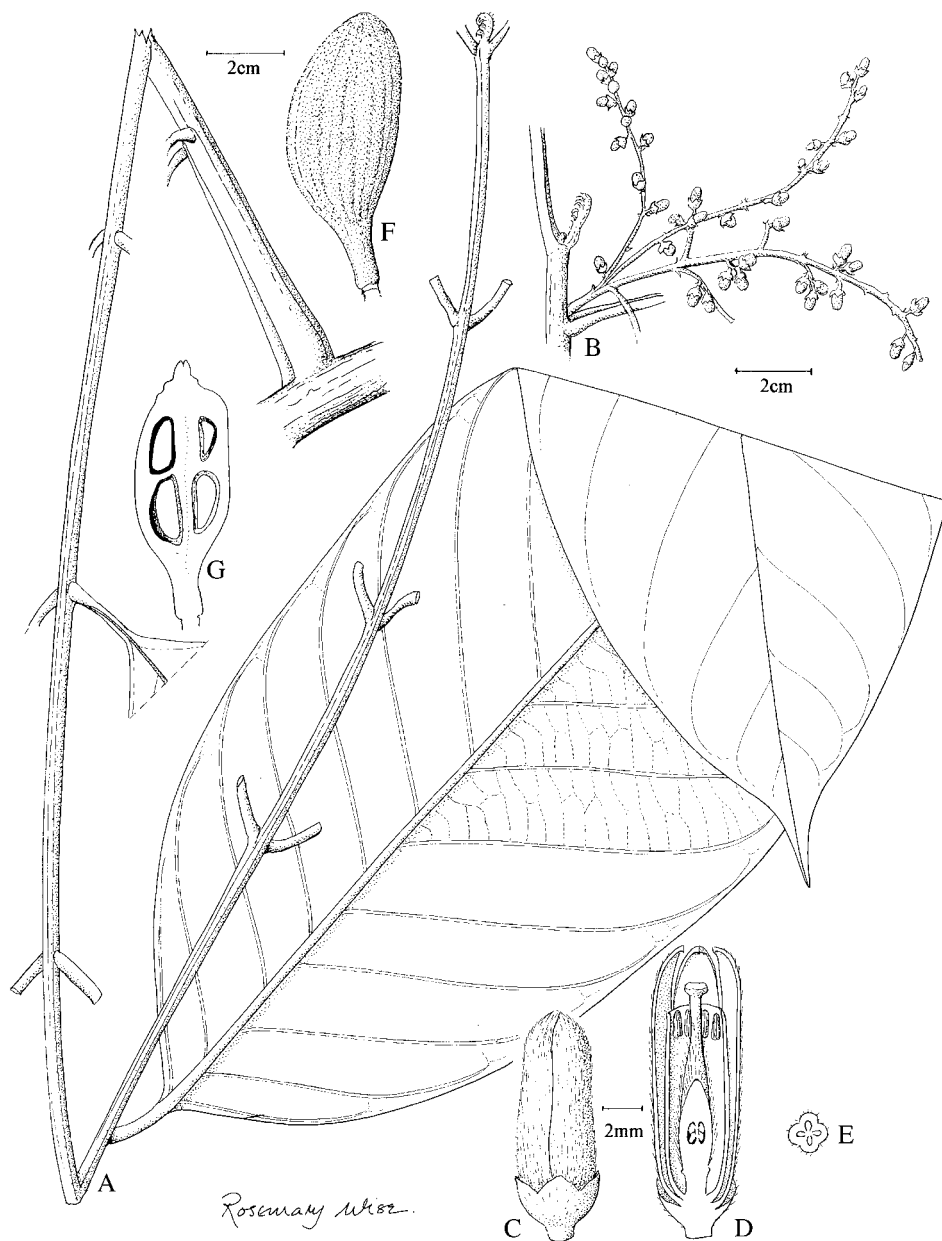


FIG. 21. *Guarea guentheri* Harms. A, habit; B, inflorescence; C, flower bud; D, half-flower; E, cross-section of ovary; F, fruit; G, longitudinal section of fruit. (A, F, G, *Palacios & Neill* 957; B, *Palacios et al.* 1180; C-E, *Krukoff* 8240).

6-14(-16) pairs, inflorescence axillary or below the leaves, (2-)8-35(-55) cm long, a slender thyrses, petals 4-5, valvate, (5-)6-9(-11) mm long, staminal tube 4.5-7(-8.5) mm long, 1.5-3(-4) mm broad, anthers 8(-10), ovary (3-)4(-5)-locular,

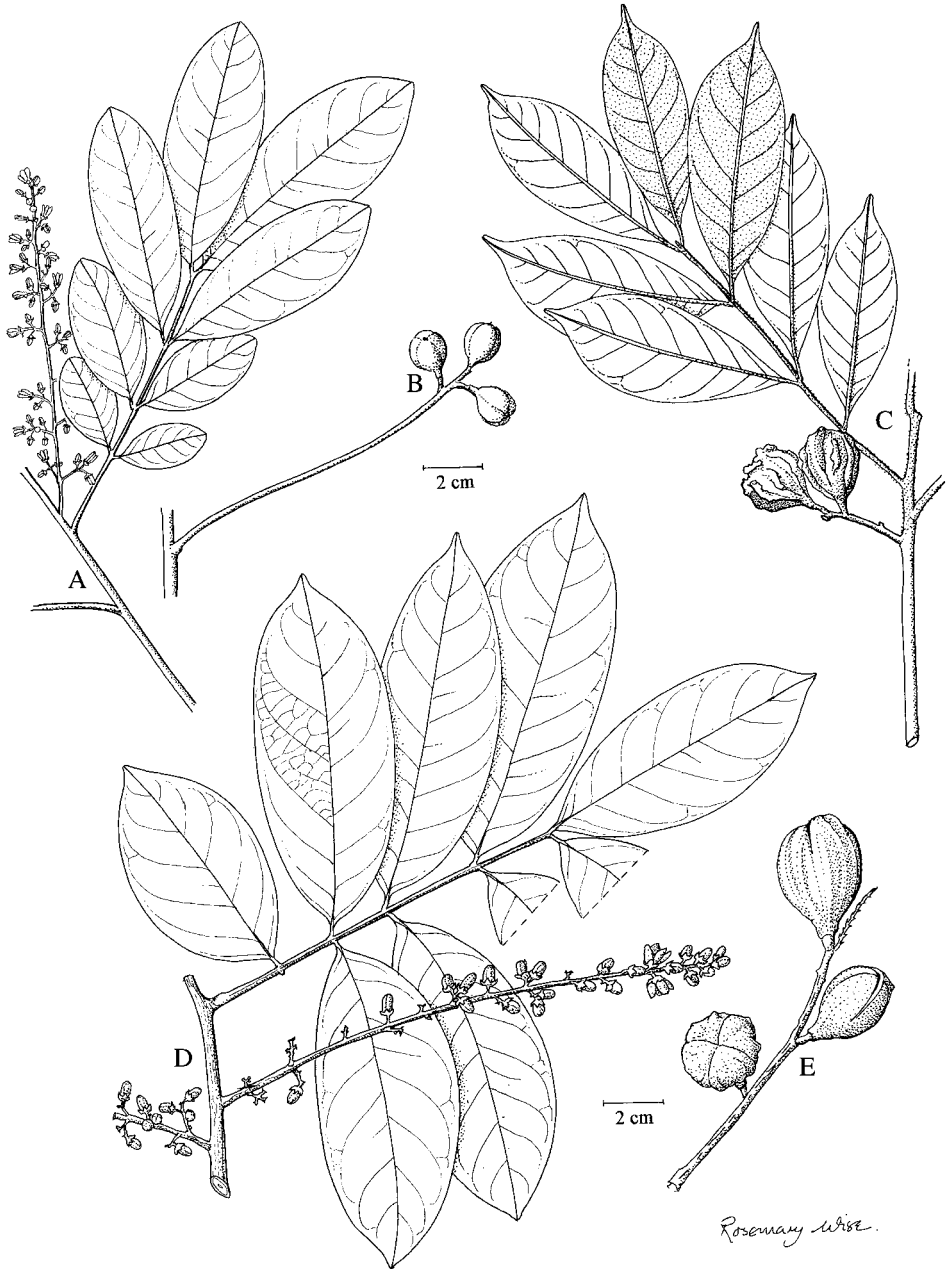


FIG. 22. *Guarea macrophylla* Vahl. A, B, subsp. *spiciflora* (A.Juss.) T.D.Penn.: A, habit; B, infructescence. C, subsp. *tuberculata* (Vell.) T.D.Penn., habit. D, E, subsp. *macrophylla*: D, habit; E, infructescence. (A, Hassler 42391; B, Zardini & Hellman 48976; C, Martinelli 1074; D, Rutkis 472; E, Beard 229).

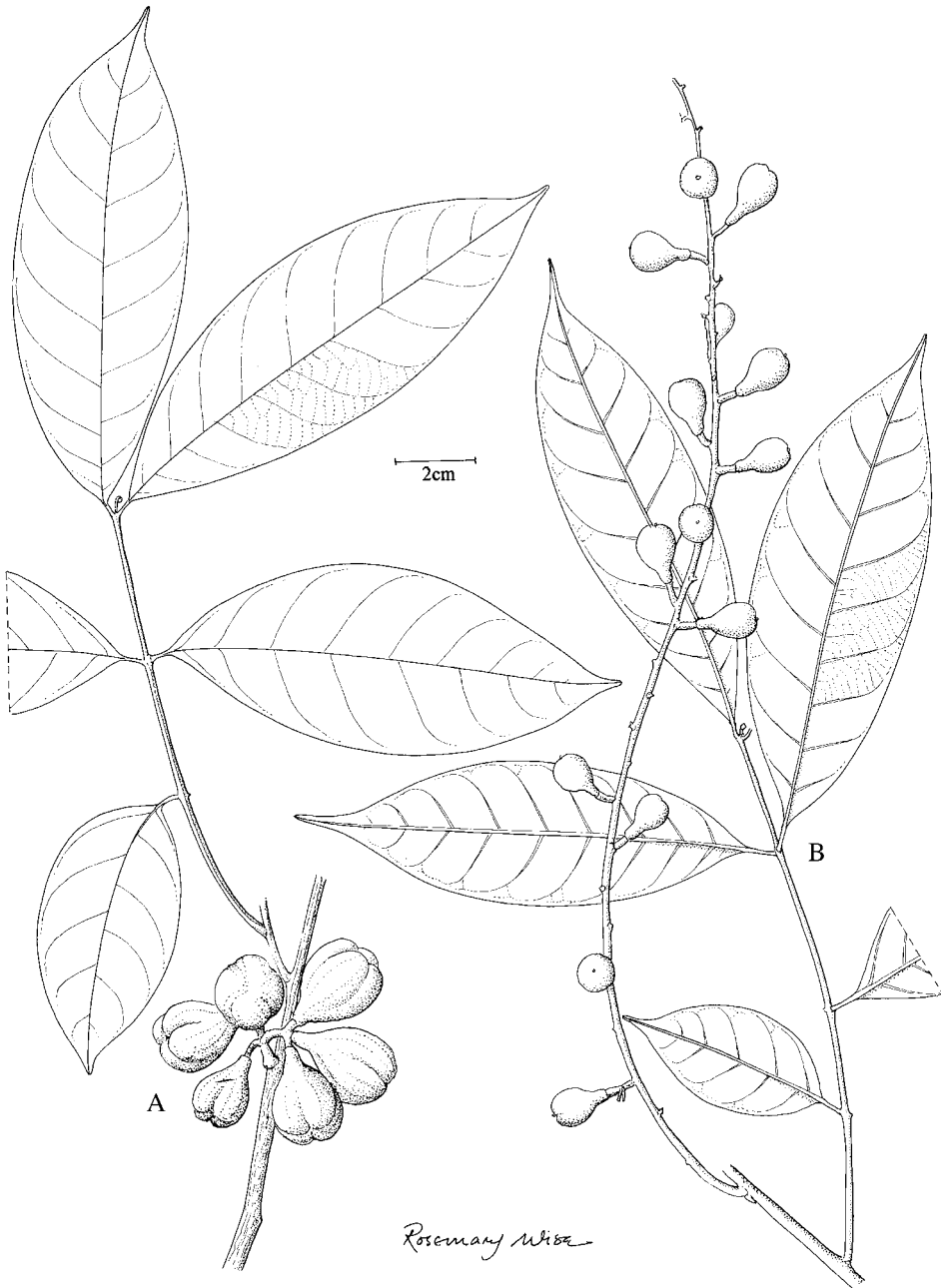


FIG. 23. *Guarea macrophylla* Vahl. A, subsp. *pachycarpa* (C.DC.) T.D.Penn., habit. B, subsp. *pendulispica* (C.DC.) T.D.Penn., habit. (A, Oldeman 1221; B, Jansen-Jacobs et al. 2487).

locules with 1–2 superposed ovules, puberulous or pubescent, capsule 0.75–3.5 cm long, depressed globose, globose or fig-shaped, usually tapering gradually to base, 4(–5)-valved, valves tuberculate, torulose, 2–3-ribbed or smooth, often wrinkling on drying, minutely puberulous to pubescent, pericarp 1–2 mm thick, valves with 1–2 superposed seeds.

28a. *Guarea macrophylla* subsp. *macrophylla*. Figs 22, 66B.

Leaflets variable in shape, \pm glabrous, without red papillae, secondary veins \pm parallel, leaves with a dormant, non-active terminal bud, inflorescence a slender thyse to 55 cm long, petals 9–11 mm long, anthers 1.25–1.5 mm long, capsule 2.5–3.5 cm long, subglobose to fig-shaped, shallowly and irregularly costulate or torulose, papillose-puberulous, valves with 1(–2) superposed seeds.

Distribution and ecology. Lesser Antilles and northern Venezuela, in lowland and lower montane rain forest up to 700 m altitude.

Additional collections examined. WINDWARD ISLANDS. **Dominica:** Syndicate Estate, GR 692157 (NW1561), *Pendry* 82204 (K).

VENEZUELA. **Yaracuy:** San Felipe, Aroa to Cocorote (NW1068), *Rutkis* 476 (K).

28b. *Guarea macrophylla* subsp. *tuberculata* (Vell.) T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 285, fig. 58 (1981). Figs 22, 63B.

Guarea tuberculata Vell., Fl. Flum. 150 (1829); Vell., Fl. Flum. 4: t. 10 (1831). – Type: [icon] Vellozo, Fl. Flum. 4: t. 10 (1831).

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 285–287 (1981).

Leaflets variable in shape, often pubescent on lower surface, sometimes with granular red papillae, secondary veins usually convergent, leaves with an active terminal bud showing intermittent growth, inflorescence usually a slender laxly-flowered thyse, occasionally with a few short branches at base, to 25(–35) cm long, petals (5–)6–9 mm long, anthers (0.75–)1–1.5 mm long, fruit (1–)1.5–3 cm long, depressed-globose to fig-shaped, usually prominently tuberculate and/or ribbed, densely to sparsely pubescent, valves with 1–2 superposed seeds.

Distribution and ecology. Eastern, central and southeastern Brazil, Paraguay, Bolivia and doubtfully in Amazonian Peru (see note below). In southeastern Brazil it occurs in lowland rain forest. Further to the north and west it appears to be confined to gallery forest in drier cerrado vegetation. Ascending to 1200 m altitude in ‘brejo’ forest in Bahia.

Representative additional collections. BRAZIL. **Bahía:** Município Lençóis, Chapadinha (SW1241), *Gasson et al.* 5880 (K). **Distrito Federal:** Município Brasília, Fazenda Sucupira (SW1547), *Sampaio et al.* 184 (K). **Espirito Santo:** Conceição da Barra, Parque Estadual de Itaunas (SW1940), *Salino & Moraes* 4489 (K). **Paraná:** Município de Jaguariaiva, Parque Estadual do Cerrado (SW2449), *von Linsingen & Sonehara* 588 (K). **Pernambuco:** São Vicente

Ferrer, Mata do Estado (SW0735), *Ferraz & Melo* 721 (K). **Rio de Janeiro:** Municipio Porati, Apa-cairucu (SW2344), *Konno* 109 (K). **São Paulo:** Socorro (SW2246), *Groppa* 874 (K).

BOLIVIA. Santa Cruz: Prov. Velasco, R. Itenez, frontier with Mato Grosso (SW1360), *Peña & Foster* 237 (K).

PARAGUAY. Paraguari: Ybycui (SW2656), *Zardini* 4960 (K, MO).

In the *Flora Neotropica* account (Pennington *et al.*, 1981), a few collections from Amazonian Peru were included in this subspecies (*Killip & Smith* 26793 (F), *Gentry et al.* 18858 (MO), *Schunke* 6895 (MO)). These possibly represent a distinct species or a form of *Guarea macrophylla* subsp. *pachycarpa*. No further collections of this plant have been made, and they remain doubtful and are excluded from the distribution map of the subspecies.

28c. *Guarea macrophylla* subsp. *spiciflora* (A.Juss.) T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 287, fig. 58 (1981). – *Guarea spiciflora* A.Juss. in St.Hil., Fl. Bras. Mer. 2: 81 (1829), as ‘*spicaeflora*’. – Type: Brazil, Rio de Janeiro, banks of the Parahyba (Paraiba) River, fl., *St. Hilaire* s.n. (holo P). **Figs 22, 51C.**

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 287–288 (1981).

Leaflets nearly always oblanceolate, apex attenuate to rounded, glabrous, without red papillae, secondary veins usually convergent, leaves with a non-active terminal bud, inflorescence a short, laxly-flowered, slender, \pm unbranched thyse, 10–15(–20) cm long, petals 5.5–7.5 mm long, anthers (0.8–)1–1.25 mm long, fruit 0.75–1.25(–1.5) cm long, \pm globose, usually smooth, sparsely and minutely puberulous, valves usually 1-seeded.

Distribution and ecology. Paraguay and northern Argentina, and extending into southeast Brazil, in seasonally dry cerrado and gallery forest.

Representative additional collections. **BRAZIL. Mato Grosso do Sul:** Porto Murinho, Fazenda Taruma (SW2157), *Hatschbach et al.* 76556 (K). **Minas Gerais:** Marlieria, Parque Estadual do Rio Doce (SW1942), *Stehmann et al.* 2969 (K).

PARAGUAY. Alto Paraná: Estancia Río Bonito (SW2554), *Zardini & Guerrero* 42693 (K). **Caazapa:** Estancia Golondrina, Ypeti (SW2555), *Zardini & Hellman* 48976 (K). **Canindiyu:** 34 km E of Villa Ygatimi, near R. Jejui-mi (SW2455), *Gentry et al.* 59372 (K). **Central:** Paraguay River around San Antonio (SW2557), *Zardini & Velazquez* 18226 (K). **Concepción:** Paso Horqueta, Río Aquidaban (SW2357), *Zardini & Tilleria* 37437 (K). **Cordillera:** between Arroyo Yhaca and General Bernadino Caballero (SW2556), *Zardini & Jara* 36521 (K). **Guaira:** Cordillera de Ybytyruzu, road Melgarejo – Antena (SW2556), *Zardini & Velazquez* 12177 (K). **Itapua:** Yacyreta Dam Island Reserve, Ana Cua (SW2756), *Zardini & Gamarra* 51888 (K). **Misiones:** Rio Tebicuary (SW2657), *Zardini & Guerrero* 40111 (K). **Paraguari:** Parque Nacional Ybicui (SW2656), *Zardini & Velazquez* 12466 (K). **San Pedro:** around Rosario (SW2457), *Zardini & Guerrero* 56815 (K).

ARGENTINA. Corrientes: Dep. Ituzaingo, Ayo Santa Isabel (SW2757), *Vanni & Radovancich* 1006 (K). **Misiones:** San Ignacio, Teyucuaré (SW2755), *Krapovichas et al.* 44152 (K).

28d. *Guarea macrophylla* subsp. *pachycarpa* (C.DC.) T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 289, figs 57, 58 (1981). – *Guarea trichilioides* L. var. *pachycarpa* C.DC. in Mart., Fl. Bras. 11(1): 184 (1878). – Type: Brazil, Para or Maranhão, fr., *Martius* s.n. (holo M). Figs 23, 64A.

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 289 (1981).

Leaflets variable in shape, \pm glabrous, without red papillae, secondary veins convergent or parallel, leaves with a dormant non-active terminal bud, inflorescence a short densely-flowered to long slender laxly-flowered thyse to 30 cm long, usually unbranched, petals 6–8 mm long, anthers 0.75–1(–1.25) mm long, fruit 1.5–2.5(–3) cm long, usually fig-shaped and tapering to base, usually smooth, less frequently torulose or costulate, papillose or puberulous, valves with 1–2 superposed seeds.

Distribution and ecology. Venezuela and French Guiana (not yet recorded from Guyana or Surinam), Amazonian and coastal Brazil, Amazonian and Pacific Ecuador, Amazonian Peru and Bolivia. Not yet recorded from Colombia. A tree of lowland rain forest on both non-flooded and periodically flooded land, up to 800 m altitude in Bolivia.

Representative additional collections. VENEZUELA. **Bolívar:** Municipio Raul Leoni, Rio Karun (NW0563), *Fernandez* 4650 (K). **Territorio Federal Amazonas:** Misión Rio Mavaca (NW0165), *Stergios et al.* 15215 (K).

FRENCH GUIANA. Rivière Compte, 75 km S of Cayenne (NW0452), *Oldeman* 1221 (K, U).

ECUADOR. **Esmeraldas:** Anchayacu, Eloy Alfaro, Mayronga (NW0079), *Pennington et al.* 14937 (K). **Pastaza:** 25 km NW of Curaray, Pozo Petrolero 'Golondrina' (SW0177), *Rubio & Gudiño* 183 (K).

PERU. **Amazonas:** Bagua Province, Imaza (SW0478), *Diaz et al.* 4180 (MO). **Loreto:** Yanomono Explorama Tourist Camp (SW0372), *Gentry et al.* 31531 (K). **Madre de Dios:** Prov. Manu, Rio Manu, Cocha Cashu (SW1171), *Núñez et al.* 14821 (F). **Pasco:** Palcazu valley, Otto Frantzen's new rozo (SW0968), *Hartshorn et al.* 2628 (K).

BRAZIL. **Acre:** Municipio Marechal Taumaturgo, R. Jurua, Reserva Estrativista do Alto Jurua (SW0972), *Daly et al.* 7625 (K). **Alagoas:** Municipio Murici, Fazenda Amora (SW0935), *Kallunki et al.* 361 (K, NY). **Amazonas:** Rio Uatuma, near mouth of R. Pitinga (SW0257), *Cid et al.* 781 (K). **Bahia:** Municipio Jussari, road Jussari to Palmeira (SW1539), *Jardim et al.* 1732 (K). **Rondonia:** Municipio Alvorada do Oeste, INCRA lines (SW1162), *Cid Ferreira* 8961 (K).

BOLIVIA. **Beni:** Prov. General Jose Ballivián, San Borja to San Ignacio (SW1466), *Pennington et al.* 13478 (K). **La Paz:** Iturrealde, Santa Fe Tacana, *Bourdy* 1823 (K). **Santa Cruz:** Velasco Province (SW1460), *Barker & Thompson* 13 (K).

28e. *Guarea macrophylla* subsp. *pendulispica* (C.DC.) T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 290, fig. 57 (1981). – *Guarea pendulispica* C.DC. in Herzog, Feddes Repert. 7: 59 (1909). – Type: Bolivia, Cunucu, fl., *Herzog* 313 (holo G). Figs 23, 64B.
For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 290 (1981).

Leaflets variable in shape, glabrous, without red papillae, secondary veins usually \pm parallel, leaves with a dormant non-active terminal bud, inflorescence unbranched, to 50 cm long, a slender densely-flowered thyse, petals 6.5–8 mm long, anthers 0.7–1 mm

long, fruit 1.5–2.5 cm long, usually globose and abruptly contracted into a short stipe, less frequently tapering in the lower half, usually smooth, sometimes wrinkled or obscurely ribbed on drying, sparsely puberulous or papillose, valves usually 1-seeded.

Distribution and ecology. Costa Rica and Panama to Venezuela and Guyana, Colombia and Ecuador (both Pacific and Amazonian drainage), Amazonian Peru, Bolivia and Brazil (including coastal Brazil). A small tree of non-flooded rain forest, often along riverbanks and occasionally in periodically flooded forest.

Representative additional collections. COSTA RICA. **Limón:** Cordillera de Talamanca, Matina (NW1083), *Herrera* 2160 (CR, K). **San José:** Carara Biological Reserve, Bijagualito (NW0984), *Zúñiga* 524 (INB, K).

PANAMA. **Darién:** Parque Nacional de Darién, Río Pucuro (NW0877), *Nevers et al.* 8386 (K).

COLOMBIA. **Antioquia:** Municipio Anorí, Anorí to Dos Bocas, km 1–9 (NW0775), *Callejas et al.* 8694 (K). **Guajira:** Municipio Río Nacha, Tomarrazon (NW1173), *Marulanda & Betancur* 2183 (K). **Valle:** Municipio Caicedonia, 7 km N of Caicedonia (NW0475), *Silverstone-Sopkin & Paz* 6783 (K).

VENEZUELA. **Amazonas:** Río Casiquiare, 2 hours from Pacibo (NW0267), *Colella et al.* 2035 (K). **Sucre:** Río Guayabo junction with Río Zumbador (NW1064), *Davidse & Gonzalez* 19280 (K).

GUYANA. Rupunumi District, Kuyuwini Landing (NW0259), *Jansen-Jacobs et al.* 2487 (K, U).

ECUADOR. **Los Ríos:** Puerta Negra, Cerro Samama, Hacienda Clementina (SW0179), *Stahl & Cornejo* 6149 (K). **Orellana:** Río Tiputini, Yasuni Scientific Station (SW0076), *Villa & Velez* 1085 (K). **Sucumbios:** Cantón Lago Agrio, Cuyabeno Reserve (SW0075), *Palacios et al.* 7904 (K). **Zamora-Chinchipe:** 30 km NE of Zamora (SW0378), *Pennington & Tenorio* 10737 (K).

PERU. **Huánuco:** Pachitea, Codo de Pozuzo (SW0975), *Foster* 9275 (K). **Madre de Dios:** Tambopata, Infierno, Hermosa Chica (SW1269), *Alexiades et al.* 450 (K). **Pasco:** Palcazu Valley, Marcial Espiritu's land (SW0968), *Hartshorn et al.* 2769 (K). **Ucayali:** Pucallpa-Tingo Maria km 86, Alexander von Humboldt Reserve (SW0875), *Maas et al.* 4487 (NY).

BRAZIL. **Acre:** Municipio Río Branco, Parque Zoobotánico (SW0967), *Figueiredo* 42 (NY). **Amazonas:** Río Uatuma, between Cachoeira Morena and Balbina (SW0257), *Cid et al.* 109 (K). **Bahía:** Municipio de Itabuna, Jucari to Palmeira km 9 (SW1539), *Callejas et al.* 1575 (K). **Goias:** Municipio Serranópolis, Poussada dos Araras (SW1851), *Alvarenga et al.* 1273 (K). **Pará:** Parque Nacional de Tapajós (SW0455), *Silva & Rosario* 3940 (K).

BOLIVIA. **Cochabamba:** Chaparé, km 18 road to El Palmar (SW1665), *Wood* 12914 (K). **La Paz:** Prov. Sud. Yungas, Alto Beni, Reserva Mocatene de Santa Ana (SW1567), *Seidel et al.* 2877 (K). **Santa Cruz:** 2 km N of Yapacani (SW1763), *Daly & Balick* 2114 (K).

29. *Guarea pendula* R.S.Ramallo, A.L.Pinheiro & T.D.Penn., *Revista Arvore* 11: 185 (1987). – Type: Brazil, Minas Gerais, Viçosa, Mata de Silvicultura, Universidade Federal de Viçosa [SW2042], fl., xii 1983, *Ramallo & Pinheiro* 2876 (holo VIC n.v.; iso K, RB n.v.). **Figs 24, 51D.**

Guarea luciae Barreiros, *Albertoa* 1: 70 (1987), **syn. nov.** – Type: Brazil, Minas Gerais, Viçosa, Mata de Silvicultura UFV, fl., *Ramallo & Pinheiro* 2876 (holo RB n.v.; iso K, VIC n.v.).

Guarea penningtoniana A.L.Pinheiro, *Revista Ceres* 38(216): 138 (1991), **syn. nov.** – Type: Brazil, Espírito Santo, Linhares, Reserva Florestal de Linhares, Companhia Vale do Rio Doce [SW1939], fl., *Folli* 635 (holo CVRD n.v.; iso K, VIC n.v.).

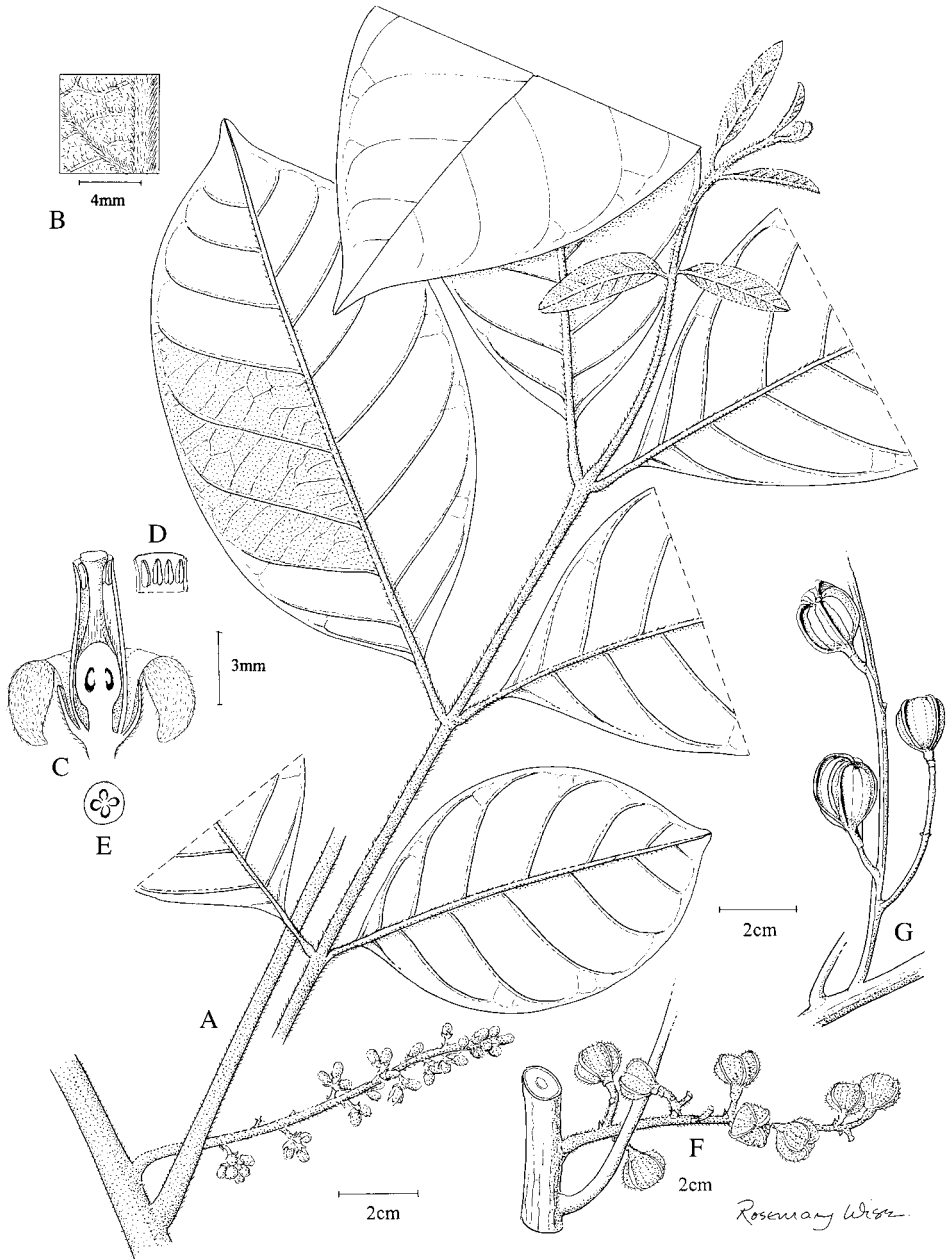


FIG. 24. *Guarea pendula* R.S.Ramalho et al. A, habit; B, enlargement of leaf undersurface; C, half-flower; D, detail of staminal tube; E, cross-section of ovary; F, young infructescence; G, mature infructescence. (A, B, Ramalho & Pinheiro 2876; C–E, Folli 700; F, Mexia 4555; G, Lopes & Andrade 502).

Young shoots golden-tomentose, 5–8 mm diam., eventually becoming glabrous, brown and suberous. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 4–15 cm long, semiterete at the base to terete at the apex, pubescent, rhachis up to 35 cm long, terete or slightly channelled above, pubescent; petiolule 5–10 mm long, pubescent. *Leaflets* up to 7 pairs, 10.5–21 × 4–8.3 cm, elliptic to oblanceolate, apex obtusely cuspidate to narrowly attenuate, base acute to narrowly attenuate, chartaceous, upper surface glabrous, but with numerous minute raised dots, lower surface with tomentose midrib and veins and softly pubescent lamina, the hairs intermixed with numerous minute red papillae, not glandular-punctate or -striate; venation eucamptodromous, midrib sunken on the upper surface, secondaries 6–10 pairs, ascending, arcuate, slightly to strongly convergent, intersecondaries short or absent, tertiaries few, oblique. *Inflorescence* axillary and on twigs below the leaves, up to 30 cm long and with indeterminate apical growth, a slender thyrses with a few lateral branches in the lower half to 7 cm long, pubescent to tomentose, flower clusters subtended by small ovate bracts 1–2 mm long; pedicel c.1 mm long. *Calyx* cyathiform, 2.5–3 mm long, 4-lobed to halfway or more, lobes ovate, pubescent outside, glabrous inside. *Petals* 4, valvate, c.8 × 2 mm, strap-shaped, apex acute, appressed pubescent outside, glabrous inside. *Staminal tube* c.7 × 1.5 mm, margin truncate, glabrous; anthers 8, c.1.25 mm long, glabrous, dehiscent. *Nectary* 1–1.25 mm long, a stout stipe supporting the ovary, glabrous. *Ovary* 2–2.5 mm long, ovoid, 4-locular, locules 1-ovulate, densely long-strigose, style 2–2.5 mm long, glabrous, style-head discoid, equalling the anthers. *Capsule* 1.5–2 cm long, c.1.5 cm broad, broadly pyriform, apex truncate, base tapering to a short stipe, 4-valved, each valve shallowly 3-costate, pubescent, becoming sparser with age, valves 1-seeded. *Seeds* c.1.5 × 1 cm, surrounded by a red sarcotesta.

Field characters. Tree to 15 m high and 20 cm diam., bark fissured and scaling in small plates, flowers cream-coloured, capsule maturing dark red, and seeds with a red sarcotesta. Flowering recorded in December and March, mature fruit in August.

Distribution and ecology. Minas Gerais and Espírito Santo, Brazil in Atlantic coastal rain forest and in drier semideciduous forest around Viçosa, up to 700 m altitude.

Collections examined. BRAZIL. **Minas Gerais:** Caratinga Biological Station (SW1942), Lopes & Andrade 502 (K).

Local names. Cedro baio (Espírito Santo), tauba, cura madre (Minas Gerais).

In its morphology *Guarea pendula* belongs in the group of species containing *G. guidonia*, *G. macrophylla* and *G. pubescens*, which are all characterised by small flowers with 4 petals, 8 anthers, and 4-locular ovary with 1-ovulate locules. It is perhaps closest to *Guarea macrophylla* but differs from it in the uniformly pubescent lower lamina, and generally smaller, obscurely ribbed fruit which is not tuberculate. However, the phylogenetic analysis places it next to *Guarea gracilis* and *G. blanchetii* (all from coastal Brazil).

30. *Guarea blanchetii* C.DC. in Mart., Fl. Bras. 11(1): 187 (1878); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 357 (1981). – Type: Brazil, Bahía, fl., *Blanchet* 2324 (holo G-DC; iso G, NY, P). **Figs 25, 51E.**

Young shoots tomentose with yellowish hairs, soon becoming glabrous and developing a thick suberous and fissured bark, 0.5–1.5 cm diam. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 10–16 cm long, channelled on the upper surface or semiterete, shortly pubescent, rhachis up to 50–60 cm long, semiterete or slightly channelled above, shortly pubescent; petiolule 4–5 mm long, swollen. *Leaflets* opposite, 2–13 pairs, 23–42 × 8.5–18.5 cm, broadly oblong or elliptic, apex acuminate to obtusely cuspidate, base acute to narrowly attenuate, lowest pair of leaflets much smaller c.8 × 5 cm, chartaceous, upper surface glabrous, lower surface with pubescent midrib and veins and with scattered hairs across the lamina, numerous minute red papillae usually present, not glandular-punctate or -striate; venation eucamptodromous, midrib slightly sunken on the upper surface, secondaries 14–16 pairs, ascending, straight or slightly arcuate, parallel or slightly convergent, intersecondaries short or absent, tertiaries oblique and parallel. *Inflorescence* cauliflorous or ramiflorous, 6–15 cm long, a slender panicle with a few short lateral branches near the base to 3 cm long, sparsely pubescent; pedicel c.1 mm long. *Calyx* cyathiform, 2.5–3 cm long, deeply and irregularly 4-lobed, lobes broadly ovate, obtuse or rounded, with scattered hairs outside, glabrous inside. *Petals* 4(–5), valvate, 7–8 mm long, 2–3 mm broad, strap-shaped, apex acute, appressed pubescent outside, glabrous inside. *Staminal tube* c.5 mm long, 1.5–2 mm broad, margin undulate, glabrous; anthers 8, c.1 mm long, oblong, glabrous, dehiscent. *Nectary* a short stipe c.0.5 mm long, expanded into a collar below the ovary, glabrous. *Ovary* narrowly ovoid, c.3 mm long, 4–9-locular, locules 1-ovulate, appressed pubescent in the lower half, glabrous above, style c.1.5 mm long, glabrous, style-head discoid. *Capsule* 2–2.5 cm long, 2.5–3 cm broad, obovoid, apex truncate or slightly depressed, tapering to an obtuse base and short, broad stipe 1–2 mm long, 4–9-valved, valves with 3 irregular and anastomosing ribs or shallow wings 3–4 mm high, densely puberulous, pericarp 1–2 mm thick (excluding the wings), valves 1-seeded.

Field characters. Small treelet to 7 m high and 10 cm diam., with creamish white to yellow flowers, and pinkish mature capsule. Flowering March to April, mature fruit in July.

Distribution and ecology. Confined to the wet coastal rain forests of Bahía and Espírito Santo, Brazil.

Collections examined. BRAZIL. **Bahía:** Municipio de Una, road Olivença – Vila Brasil (SW1439), *de Carvalho et al.* 678 (K); Municipio de Urucuca, km 7.3 road Serra Grande to Itacaré (SW1439), *de Carvalho et al.* 3403 (NY); Municipio de Una, Mico-leão Biological Reserve (SW1539), *Hage et al.* 2374 (K), *Jardim et al.* 225 (NY); Municipio de Una, km 19 road Sao José de Buerarama to Una (SW1539), *Mattos Silva et al.* 719 (K); Municipio de Una, Una to Canavieiras km 5 (SW1539), *Mattos Silva et al.* 740 (K); Municipio Wenceslau

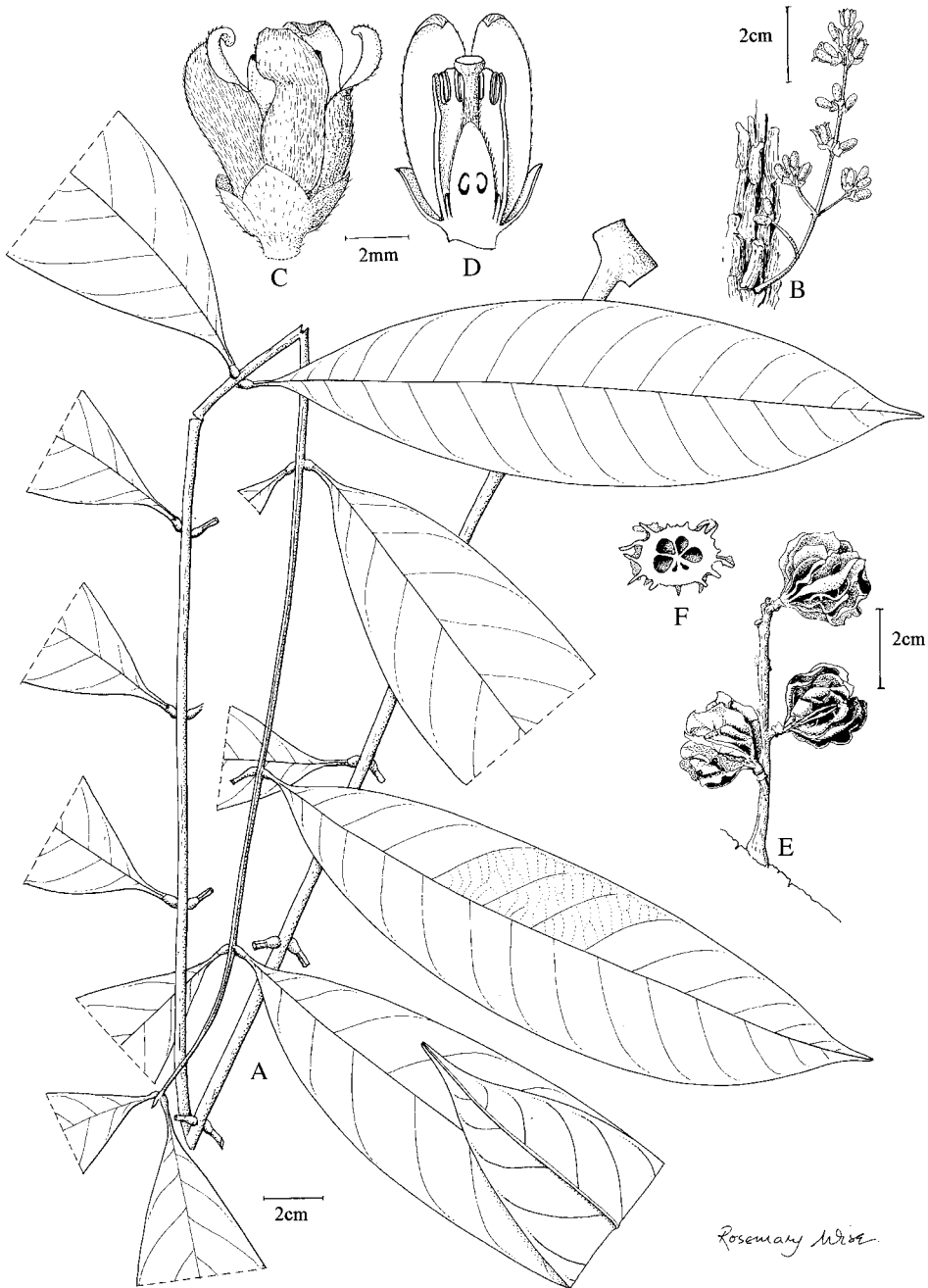


FIG. 25. *Guarea blanchetii* C.DC. A, habit; B, inflorescence; C, flower; D, half-flower; E, infructescence; F, cross-section of fruit. (A–D, *Kallunki et al.* 585; E, F, *Mattos Silva & Sant'ana* 2933).

Guimaraes, State Reserve, *Mattos Silva et al.* 2933 (NY); Municipio de Itacare, 25 km SE of Ubaitaba (SW1438), *Mori & Carvalho* 12009 (K); Municipio Ilheus, 3 km N of Rodoviaria (SW1439), *Thomas et al.* 10591 (NY); Divisa da Fazenda Maruim com Faz. Dois de Julho, 40 km S of Ilheus (SW1539), *Sant'Ana et al.* 360 (NY). **Espirito Santo:** Municipio Rio Bananal, Faz. Lagoa Santa, W of Linhares (SW1940), *Kallunki et al.* 585 (G, MO, NY).

Local name. Bilveiro-cortica.

The floral structure of *Guarea blanchetii* is similar to that of many small-flowered species such as *G. guidonia*, *G. convergens* and *G. macrophylla*, with 4 valvate petals, 8 anthers and a 4-locular ovary with 1-ovulate locules. It is however distinctive in its cauliflorous inflorescence, in the variable number of ovary locules and prominently ribbed capsule. The capsule is similar to that of *Guarea velutina* and *G. juglandiformis*, but the ribs are shallower, and it also differs from those species in its cauliflorous inflorescence and much larger leaflets. The present delimitation of *Guarea blanchetii* is problematic, as the ITS phylogeny indicates that it contains a high amount of intra-specific variation, and has *G. gracilis* embedded within it.

31. *Guarea gracilis* T.D.Penn., sp. nov. Figs 26, 51F.

Guarea macrophyllae affinis sed foliolis gracilioribus, capsula manifeste costata differt. – Type: Brazil, Rio de Janeiro, Rio das Ostras, Uniao Biological Reserve, fr., May 1998, *P.P. de Oliveira* 344A (holo K; iso BHCB n.v.).

Young shoots sparsely short-pubescent, soon glabrous, smooth, greyish, 2–3 mm diam. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 2–4 cm long, semiterete, glabrous, rhachis 7–12.5 cm long, semiterete, glabrous; petiolule c.3 mm long, slightly channelled on the upper surface, glabrous. *Leaflets* opposite, 2–5 pairs, uppermost pair 9–13.5 × 2–3 cm, lowermost pair 4–5 × 2–2.3 cm, narrowly elliptic to elliptic, apex acuminate, base narrowly attenuate, chartaceous, glabrous above, scattered appressed hairs on midrib below and sparse minute red papillae on the lamina, not glandular-punctate or -striate; venation eucamptodromous, midrib sunken on the upper surface, secondaries 6–8 pairs, ascending, arcuate, convergent, intersecondaries moderately long, tertiaries perpendicular to coarsely reticulate. *Inflorescence* axillary, 8–13 cm long, a very slender panicle with some short lateral branches near the base, few- and lax-flowered, sparsely appressed puberulous. *Flowers* subtended by small ovate bracts c.1 mm long; pedicel c.1 mm long. (Flower buds only seen.) *Calyx* cup-shaped, c.1 mm long, with 4 triangular lobes about 1/3 of its length, sparsely appressed puberulous outside, glabrous inside. *Petals* 4, c.1.5 mm long (in bud). *Staminal tube* with 8 anthers in the throat. *Ovary* 4-locular, strigose, locules 1-ovulate; style-head discoid. *Capsule* 1.2–1.5 cm long, 1.7–2 cm broad, depressed-globose, apex truncate, base obtuse, 4-valved, the valves prominently longitudinally 3-ribbed, the 2 lateral ribs more prominent than the central one, 2–3 mm high, the central rib smaller and shallower, pericarp c.1.5 mm thick (between the ribs), sparsely puberulous; each valve with a solitary seed, c.1.1 × 0.8 cm, shaped like the segment of an orange, completely surrounded by a thin fleshy

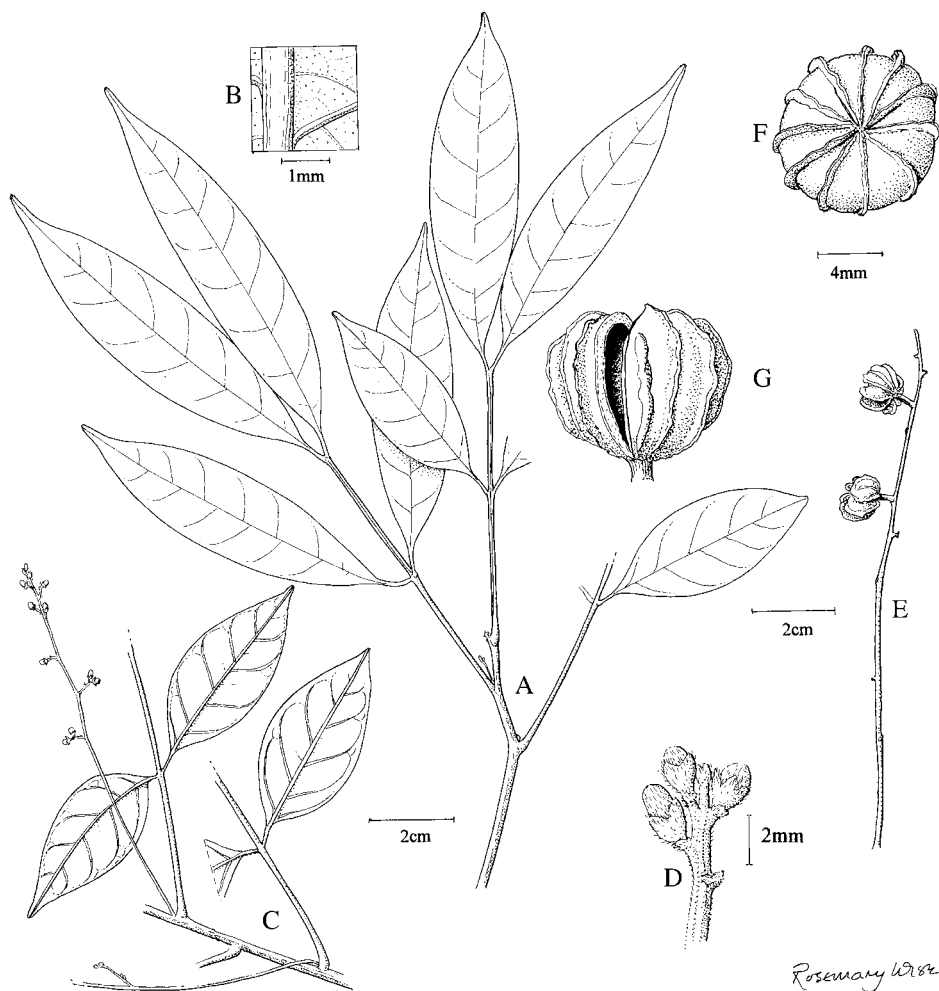


FIG. 26. *Guarea gracilis* T.D.Penn. A, habit; B, enlargement of leaf underside; C, inflorescence; D, flower buds; E, infructescence; F, fruit. (A–D, *Oliveira* 647B; E, F, *Oliveira* 344A).

sarcotesta. *Seed coat* thin and fleshy; embryo with plano-convex, superposed cotyledons, radicle abaxial, extending to the surface; endosperm absent.

Field characters. A small understory treelet with dark red fruit. Young flowers collected in November and December, fruit in May, July and September.

Distribution and ecology. In wet hill forest in Rio de Janeiro and Espirito Santo, Brazil.

Collections examined. BRAZIL. **Espirito Santo:** Linhares, Linhares Forest Reserve (SW1939), *Folli* 1427 (K). **Rio de Janeiro:** Rio das Ostras, União Biological Reserve (SW2141), *de Oliveira* 65E (K), 647 (K), 647B (K).

Morphologically closest to *Guarea macrophylla* and *G. pendula*, but clearly distinct on the basis of the slender leaflets with few (6–8) secondary veins, and the small depressed-globose capsule with prominent longitudinal ribs. The flowers have the same basic structure as those of *Guarea macrophylla*, but are probably smaller (flowers seen only in bud). This relationship is supported by the ITS phylogeny.

One further collection from Caratinga, Minas Gerais (*Horta et al.* 316 (K)) probably belongs in this species.

32. *Guarea carapoides* Harms, Notizbl. Bot. Gart. Berlin-Dahlem 10: 245 (1928); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 333 (1981). – Type: Peru, Amazonas, mouth of R. Santiago, fl., *Tessmann* 4376 (holo B, destroyed; photo F; iso F (fragment)). **Figs 27, 53D.**

Young shoots massive, 2–3 cm diam., glabrous, dark brown, smooth at first, soon becoming suberous and fissured (bark 3–4 mm thick). *Leaves* pinnate, petiole 28–33 cm long, strongly channelled and winged at the base, glabrous, rhachis 40–50 cm long, semiterete, glabrous, petiolule c.1 cm long, strongly swollen, glabrous, leaflets opposite, 5–7 pairs, 35–38 × 10–11 cm, oblong to oblanceolate, apex acuminate, base acute to rounded, subcoriaceous, glabrous, not glandular-punctate or -striate; venation eucamptodromous, midrib sunken on the upper surface, secondaries 12–16 pairs, ascending, parallel or slightly convergent, mostly straight, intersecondaries absent, tertiaries oblique, fine, numerous. *Inflorescence* axillary or on twigs below the leaves, 13–30 cm long, a slender panicle with short lateral branches to 1 cm long, or racemose, minutely puberulous. *Flowers* subtended by minute bracts; pedicel 1–2 mm long. *Calyx* cup-shaped in bud, becoming patelliform, 4–5 mm long, c.10 mm wide, margin irregularly lobed and divided, lobes rounded, finely puberulous outside, glabrous inside. *Petals* 5–6, valvate, c.1.7 × 0.3–0.4 cm, strap-shaped, apex acute, finely appressed pubescent outside, glabrous inside. *Staminal tube* c.1.2 × 0.5 cm, cylindrical, margin entire, glabrous; anthers 10–12, c.1.5 mm long, oblong, glabrous. *Nectary* a stout stipe, c.1.5 mm long, expanded into a collar below the ovary, glabrous. *Ovary* ovoid, 9–12-locular, locules with 2 superposed ovules, pubescent, style pubescent, tapering gradually to the discoid stigma. *Capsule* c.7.5 × 5.5 cm, pyriform, apex truncate, tapering to an acute base, 9–12-valved, when dry each valve with a single faint longitudinal rib (probably smooth when fresh), finely puberulous, valves with 1–2 superposed seeds, pericarp 1–1.5 cm thick. *Seed* 1–1.5 cm long.

Field characters. Tree to 14 m high and 10 cm diam. *Flowers* with a red calyx and pinkish corolla. Flowering recorded in July and August, mature fruit in November.

Distribution and ecology. Western Amazonian Brazil, Amazonian Peru and Ecuador in non-flooded lowland rain forest over clay, up to 400 m altitude.

Collections examined. ECUADOR. **Orellana:** Yasuní National Park, Maxus road km 20 (SW0076), *M. Aulestia* & *Grefa* 185 (QCNE).

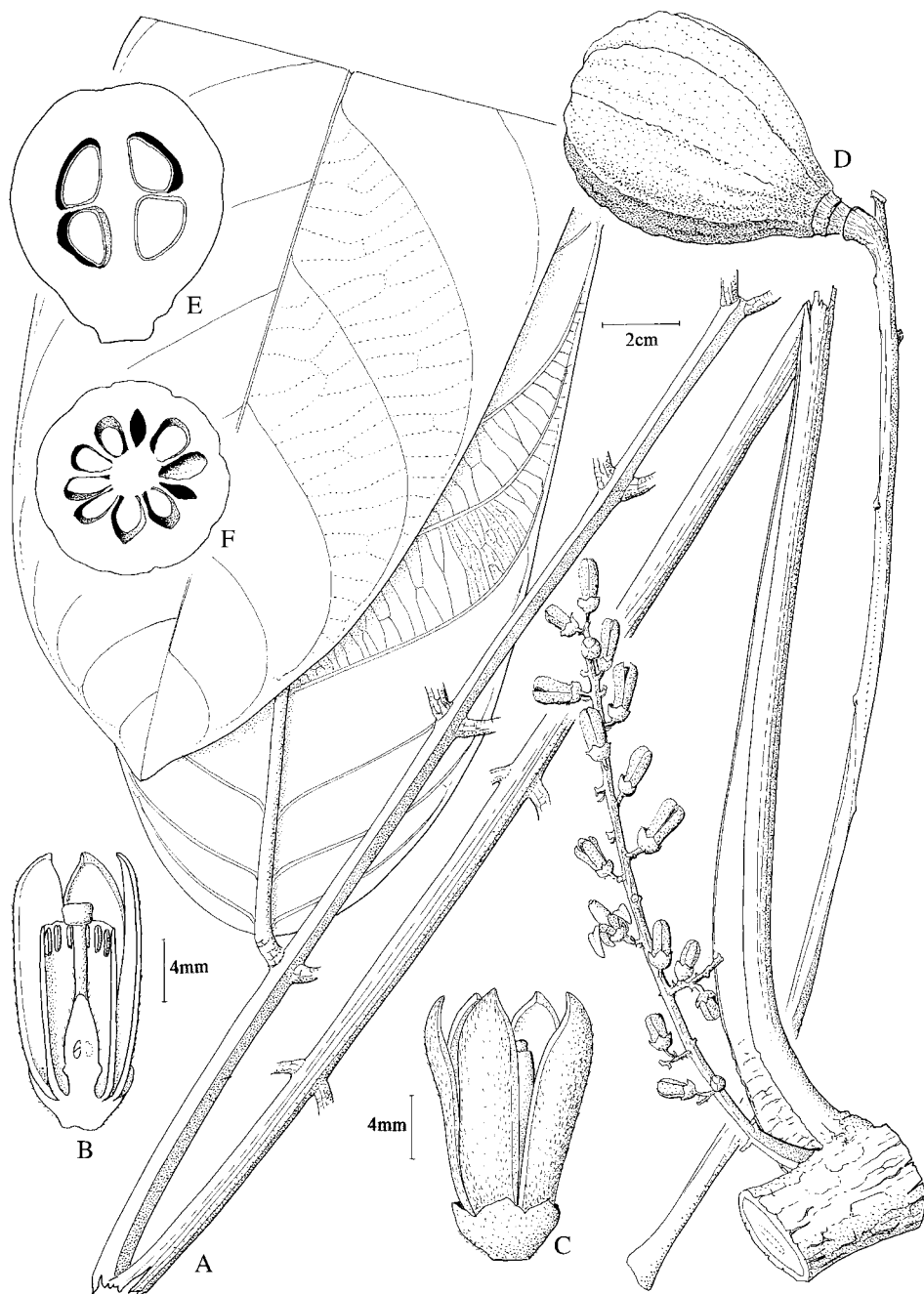


FIG. 27. *Guarea carapoides* Harms. A, habit; B, half-flower; C, flower; D, fruit; E, longitudinal section of fruit; F, cross-section of fruit. (A–C, *Ferreira et al.* 5132; D, E, *Tunqui* 56; F, *Berlin* 3581).

PERU. **Amazonas:** E bank of Santiago River, Galilea (SW0477), *Berlin* 3581 (MO); Distrito Imaza, Bagua Province, Yamayakat, *Diaz et al.* 7864 (QCNE); River Cenepa, Huampani (SW0478), *Kujikat* 317 (MO); Condorcanqui Province, Distrito el Cenepa, Tutino (SW0478), *Rojas et al.* 45 (F); River Santiago, Caterpiza (SW0377), *Tunqui* 56 (MO); Alto Amazonas, R. Huallaga, Shucushuyacu (SW0675), *Vásquez & Jaramillo* 2454 (MO); Bagua, Yamayakat, track to Putuim (SW0478), *Vásquez & Jaramillo* 20267 (K); Distrito el Cenepa, Pagki-Suwa (SW0478), *Vásquez et al.* 22169 (F).

BRAZIL. **Acre:** Municipio Cruzeiro do Sul, BR 364, INCRA Reserve (SW0772), *Cid Ferreira et al.* 5132 (NY).

33. *Guarea ecuadoriensis* W.Palacios, *Novon* 4: 160, fig. 4 (1994). – Type: Ecuador, Napo, Coca, Reserva Florística El Chuncho [SW0077], fl., *Palacios* 1633 (holo QCNE; iso K, MO). **Figs 28, 53E.**

Young shoots massive, 1–3 cm diam., densely golden tomentose or velutinous. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 18–35 cm long, massive, strongly channelled and winged at the base, densely tomentose, rhachis up to 1 m long, strongly channelled, densely tomentose; petiolule swollen, 1–2 cm long. *Leaflets* opposite, up to 15 pairs, 30–66 × 10–18 cm, broadly oblong, apex obtuse or obtusely cuspidate, base truncate or slightly cordate, upper surface pubescent along the midrib and veins, lower surface tomentose, indumentum sparser on the lamina, thinly coriaceous, not glandular-punctate or -striate; venation eucamptodromous, midrib sunken on the upper surface, secondaries 25–33 pairs, shallowly ascending, straight, parallel or lowermost slightly divergent, very prominent on the lower surface, intersecondaries mostly absent, tertiaries oblique, often obscure. *Inflorescence* axillary or in the axils of fallen leaves, a pendulous panicle 30–100 cm long, with a few lateral branches near the base to 20 cm long, tomentose; pedicel c.1 mm long above the articulation. *Calyx* 7–10 mm long, deeply and irregularly 3–4-lobed to halfway or more, appressed puberulous outside, glabrous inside. *Petals* 5–6, 18–20 mm long, 3–4 mm broad, strap-shaped, apex acute, pale-sericeous outside, glabrous inside. *Staminal tube* 13–15 mm long, 4–5 mm broad, margin entire, glabrous; anthers 13–14, c.2.5 mm long, glabrous. *Nectary* a stout stipe c.3 mm long, expanded at the apex. *Ovary* (male only seen) c.3 mm long, ovoid, 7–9-locular, locules with 2 superposed ovules, densely pubescent, style c.7 mm long, sparsely pubescent, style-head broadly discoid, equalling the anthers. *Capsule* 5–6 × 3.5–6 cm, broadly oblong to obovoid, apex rounded to truncate, base obtuse or tapering to a short stipe, smooth (slightly ribbed when dry), 7–9-valved, pericarp c.1 cm thick, densely tomentose, valves with 2 superposed seeds. *Seeds* 1.3–2 cm long; embryo with plano-convex, superposed cotyledons.

Field characters. Tree to 30 m high, little-branched, the branches with terminal clusters of very large leaves. Flowers with cream-coloured corolla, the margins of the petals sometimes pinkish, fruit maturing red. Flowering in June, mature fruit in September and October.

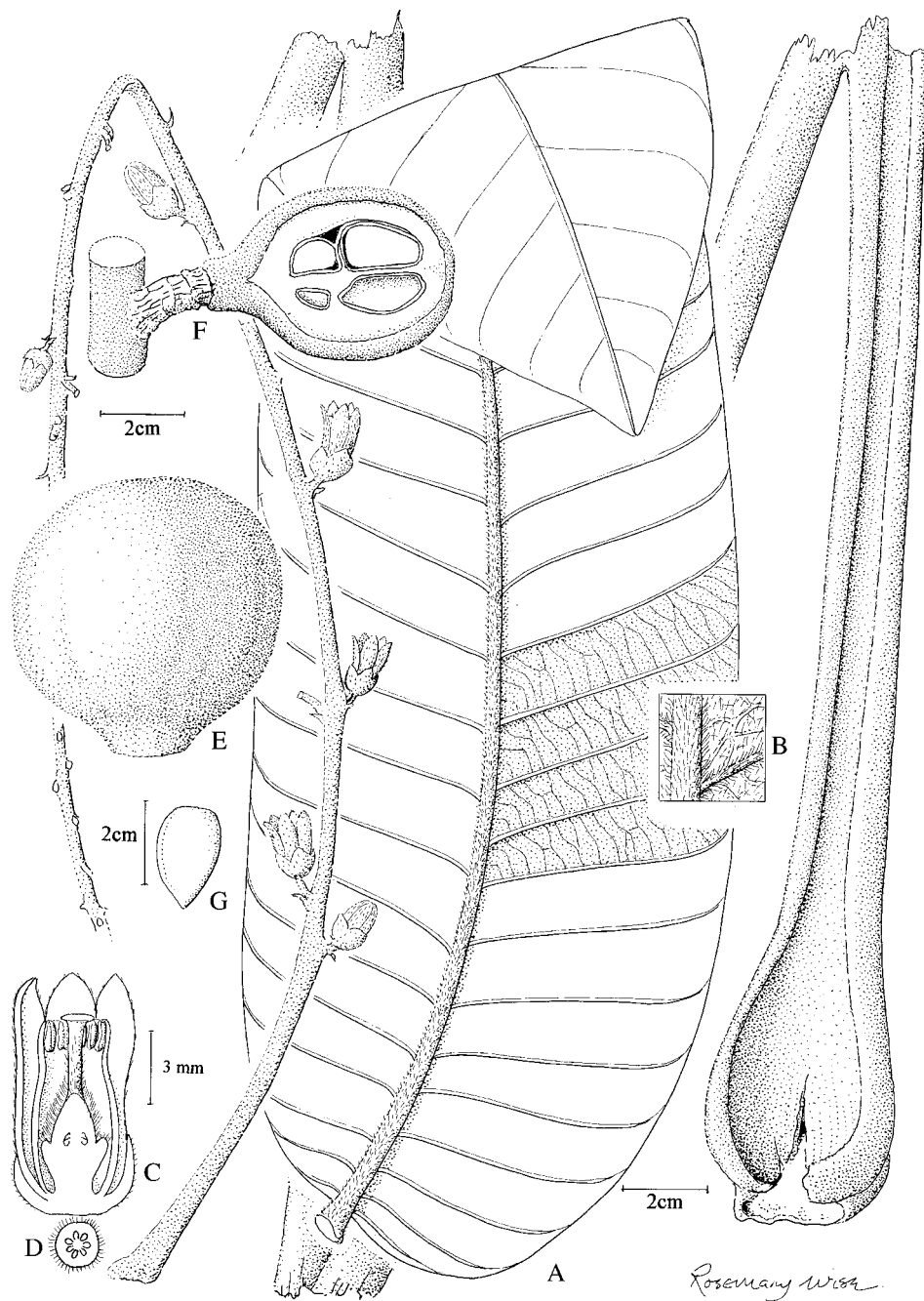


FIG. 28. *Guarea ecuadoriensis* W. Palacios. A, habit; B, enlargement of leaf undersurface; C, half-flower; D, cross-section of ovary; E, fruit; F, longitudinal section of fruit; G, seed. (A–D, Palacios *et al.* 1285; E, G, Rudas & Prieto 3164; F, Vásquez & Soto 8324).

Distribution and ecology. Amazonian Colombia, Ecuador and Peru and extreme western Amazonian Brazil. A tree of lowland rain forest on non-flooded land below 400 m altitude.

Collections examined. COLOMBIA. **Amazonas:** Leticia, Parque Nacional Natural Amacayacu (SW0370), *Rudas & Prieto* 3164 (MO).

ECUADOR. **Orellana:** Estación INIAP Payamino, Reserva 'El Chunchu' (SW0077), *Palacios et al.* 1285 (NY, QCNE); 5 km N of Coca, Coca–Payamino road (SW0077), *Palacios* 3193 (K); Añangu, Yasuní National Park (SW0076), *SEF* 8728 (K, NY).

PERU. **Loreto:** Maynas, Quebrada Sucursari (SW0372), *Gentry et al.* 42655 (AMAZ, K); Maynas, Iquitos–Nauta, km 42 (SW0473), *Vásquez & Soto* 8324 (MO); Maynas, Allpahaayo (SW0473), *Vásquez et al.* 6599 (MO).

BRAZIL. **Acre:** Município Cruzeiro do Sul, Seringal São João, Tapauna (SW0972), *Daly et al.* 7526 (K, NY).

A very distinctive species characterised by the very large leaflets, tomentose indumentum on all parts of the plant and very large flowers. Morphologically it is closest to *Guarea grandifolia*, but it has larger leaflets with more numerous secondary veins, larger flowers and tomentose fruit. The dense tomentose indumentum is also unusual, though not unknown, in *Guarea grandifolia*.

34. *Guarea fistulosa* W.Palacios, Fl. Ecuador 82, Fam. 98, Meliaceae: 25 (2007) (nom. nov.). – *Guarea penningtoniana* M.E.Morales, Rev. Acad. Colomb. Cienc. Exact. Fis. Nat. 84: 339 (1998), non *Guarea penningtoniana* A.L.Pinheiro. – Type: Colombia, Guaviare–Caquetá, Parque Nacional Chiribiquete [NW0072], fr., *Barbosa et al.* 8090 (holo COL; iso COL, K). **Figs 29, 54A.**

Young shoots finely appressed puberulous at first, soon glabrous, smooth, not scaling, brown, 1.3–1.8 cm diam., hollow. *Leaves* pinnate with an inactive terminal bud, without intermittent growth, petiole 20–30 cm long, strongly channelled at the base, semiterete above, subglabrous, rhachis 30–40 cm long, terete, glabrous; petiolule 5–20 mm long, usually swollen. *Leaflets* opposite, 4–7 pairs, (18–)30–52.5 × (4.5–)5.7–13.5 cm, lower pairs often much smaller, oblong or oblanceolate, apex narrowly attenuate, base acute to narrowly cuneate, chartaceous to thinly coriaceous, upper surface smooth, both surfaces ± glabrous, minute red glandular papillae sometimes present on the lower surface, obscurely glandular-punctate and -striate; venation eucamptodromous, midrib flat or slightly sunken on the upper surface, secondaries 18–28 pairs, ascending, usually straight and ± parallel, intersecondaries absent, tertiaries oblique, parallel. *Inflorescence* ramiflorous (on smaller branches), a slender thyse 4–8 cm long, lateral branches < 1 cm long, appressed puberulous, flower clusters subtended by small navicular, ovate bracts 1–1.5 mm long; pedicel 1–1.5 mm long (above the articulation). *Calyx* shallowly cup-shaped, 2–3 mm long, irregularly and shallowly 3–5-lobed to halfway, with scattered minute appressed hairs outside, glabrous inside. *Petals* 4(–5), valvate, 10–13 mm long, 2–3 mm broad, strap-shaped, apex obtuse, free, valvate, sericeous outside, glabrous inside.

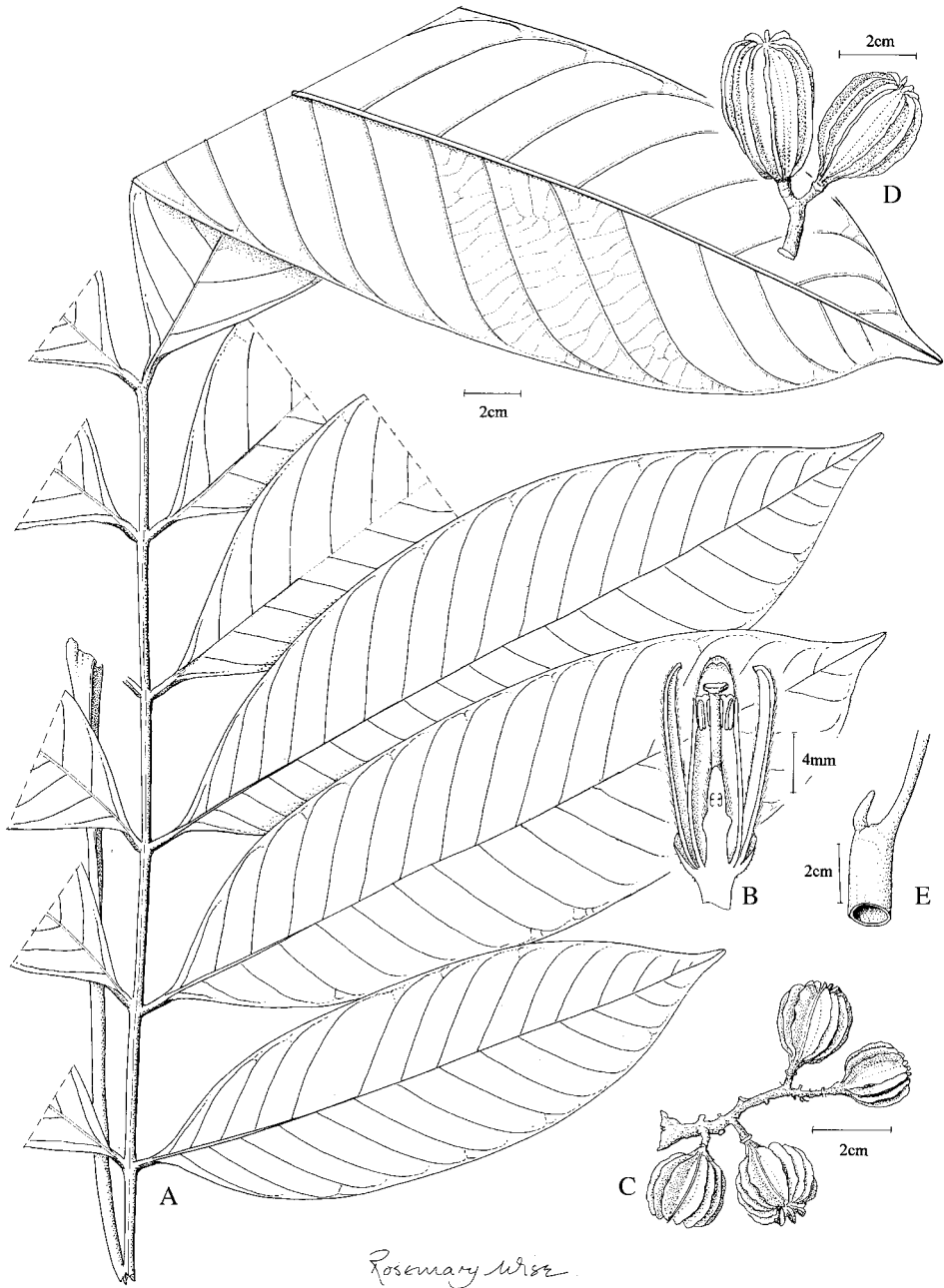


FIG. 29. *Guarea fistulosa* W. Palacios. A, habit; B, half-flower; C, infructescence; D, mature fruit; E, detail of hollow stem. (A, C, E, Palacios & Tipaz 9135; B, McPherson 10458; D, Vásquez & Jaramillo 4710).

Staminal tube 8 × 2–10 × 3 mm, margin undulate, glabrous; anthers 8, c.1.5 mm long, oblong, glabrous. *Nectary* a stipe below the ovary 1.5–2 mm long. *Ovary* narrowly ovoid, c.3 mm long, 4–5-locular, locules with 2 superposed ovules, densely pubescent, style c.5 mm long, pubescent below, glabrous near the apex, style-head discoid. *Capsule* 2.5–4 × 2.3–3 cm, broadly pyriform, apex truncate, base obtuse to rounded, 4-valved, valves with 3 longitudinal undulate ribs, 2–4 mm deep, pericarp 2–3 mm thick (excluding the ribs), shortly velutinous, valves with 1–2 superposed seeds. *Seeds* c.1.3–1.4 cm long, c.0.8 cm broad, truncate at base or apex due to compression, cotyledons plano-convex, obliquely superposed, radicle abaxial, extending to the surface. Seed surrounded by a thin fleshy sarcotesta.

Field characters. Treelet or small tree to 10 m high, often monocaulous, flowers whitish, fruit maturing red or violet. Flowering recorded in April and June, mature fruit mostly November to January.

Distribution and ecology. Panama, Amazonian Colombia, Ecuador, Peru and western Amazonian Brazil. A small understorey treelet of non-flooded lowland rain forest, below 400 m altitude.

Collections examined. PANAMA. **Bocas del Toro:** above Chiriquí Grande, 10 miles from continental divide (NW0882), *McPherson* 10458 (MO). ? **Colón:** Coclé del Norte (NW0980), *Hammel* 4567 (MO) (included with reservations).

COLOMBIA. **Amazonas:** Corregimiento de Araracuara, Puerto Arturo (SW0072), *Aguirre-Galviz* 922 (COL).

ECUADOR. **Orellana:** near Puerto Itaya, Indillama (SW0076), *Carillo* 397 (QCNE); Yasuní National Park, Maxus road km 46 (SW0076), *Dik* 344 (K); Huaorani Reserve, Miwaguno (SW0076), *Freire & Naranjo* 682 (K); Yasuní Scientific Station, Rio Tiputini (SW0076), *Romoleroux & Pitman* 2292 (K); *Romoleroux & Villa* 2390 (F, K). **Sucumbios:** Lago Agrio Canton, Cuyabeno Reserve (SW0076), *Palacios & Tipas* 9135 (MO, QCNE).

PERU. **Amazonas:** Bagua Province, Imaza, Yamayakat (SW0478), *Jaramillo et al.* 359 (F, K); Condorcanqui Prov., Tutino (SW0478), *Rojas et al.* 56 (QCNE). **Loreto:** Maynas, Puerto Almendras (SW0373), *Acevedo-Rodríguez et al.* 1621 (NY); Loreto, Tigre, Rio Tigre, Nuevo Canaan (SW0474), *Ayala et al.* 2515 (AMAZ, MO); Rio Corrientes, Teniente Lopez (SW0276), *Beltran & Foster* 709 (F); Maynas, Rio Yaguasyacu, Borro (SW0371), *Gentry & Revilla* 20451 (F, MO); Puerto Almendras, Maynas Province (SW0373), *Grandez* 2191 (QCNE); Maynas, Allpahuayo (SW0373), *Grandez & Jaramillo* 781 (MO); Maynas, Rio Nanay, Caserio Lupuna (SW0373), *Revilla* 2087 (MO); vicinity of Iquitos (SW0373), *Revilla* 3668 (F, K, NY), 3690 (K); Maynas, Mazan, Rio Amazonas (SW0373), *Rimachi* 3050 (K); Iquitos, Puerto Almendras (SW0373), *Rueda & Ruiz* 693 (MO); Prov. Requena, (surroundings) (SW0573), *Vásquez & Jaramillo* 4710 (K); Maynas, Callicebus Rio Nanay-Mishana Biological Station (SW0373), *Vásquez et al.* 2809 (MO), *Vásquez et al.* 18337 (MO).

BRAZIL. **Amazonas:** Municipio de São Paulo de Olivença, Bom Fim (SW0368), *Cid et al.* 8604 (NY); Municipio Labrea, 2–3 km SW of Labrea (SW0764), *Prance et al.* 7992 (K).

This widespread western Amazonian species has been confused with both *Guarea velutina* and *G. juglandiformis*. It differs from both in its stouter hollow twigs, larger leaves and leaflets, numerous (18–28 pairs) ± straight and parallel secondary veins,

shorter, ramiflorous inflorescence, longer petals, ovary locules with 2 superposed ovules and capsule valves with narrower, less anastomosing ribs.

There are several other species of *Guarea* similar to *G. fistulosa*, but as they are still imperfectly known, we have not yet been able to describe them.

35. *Guarea riparia* W.Palacios, Novon 4: 158, fig. 3 (1994); W.Palacios, Fl. Ecuador 82, Fam. 98, Meliaceae: 42 (2007). – Type: Ecuador, Zamora-Chinchi, Punta de Pachicutza, between Pachicutza and Miazí, banks of the R. Nangaritzá, fl., Palacios 8444 (holo QCNE; iso MO, QCA). **Figs 30, 54B.**

Young shoots finely appressed pubescent at first, soon glabrous, 2–4 mm diam., smooth, greyish brown, with a few lenticels. *Leaves* pinnate with terminal bud with intermittent growth, petiole 1.5–3.5 cm long, semiterete, sparsely pubescent, rachis 4–17 cm long, semiterete, subglabrous; petiolule 4–9 mm long. *Leaflets* 2–7 pairs, 6–14.2 × 0.9–2.8 cm, narrowly elliptic, apex long, slender acuminate, base acute to narrowly attenuate, chartaceous, glabrous, not glandular-punctate or -striate; venation eucamptodromous, midrib not raised on the upper surface, secondaries 7–10 pairs, steeply ascending, arcuate and convergent, intersecondaries short to moderately long, tertiaries obscure, oblique. *Inflorescence* axillary, 7–22 cm long, a slender many-flowered thyrse with short lateral branches 1–3 cm long, sparsely short-pubescent; pedicel 1–1.5 mm long (above the articulation). *Calyx* patelliform, 0.5–1 mm long, shallowly 4-lobed or margin truncate, with scattered minute appressed hairs outside, glabrous inside. *Petals* 4, valvate, 4–4.5 mm long, c.1.5 mm broad, strap-shaped, apex acute, appressed puberulous outside, glabrous inside. *Staminal tube* 3–3.5 mm long, c.2 mm broad, urceolate, margin undulate, glabrous; anthers 8, c.0.75 mm long, glabrous; antherodes in female smaller, c.0.5 mm long, not dehiscent, without pollen. *Nectary* c.1 mm long, a stout stipe expanded below the ovary, glabrous. *Ovary* ovoid, c.1.5 mm long, 4-locular, locules 1-ovulate, puberulous, style (in male) c.1.5 mm long, in female c.1 mm long, glabrous, style-head discoid. *Capsule* 0.9–1 cm long, 0.9–1.2 cm broad, depressed-globose, apex truncate, base truncate to obtuse, 4-valved, smooth, subglabrous, pericarp 0.5–1 mm thick, valves 1-seeded. *Seed* 7–8 mm long, plano-convex, radicle abaxial, extending to the surface; endosperm absent.

Field characters. Shrub or small tree 1–8 m high, with the young foliage opening reddish. Flowers with reddish calyx and cream-coloured corolla, fruit maturing reddish. Flowering is recorded mainly from October to December, with mature fruit in February, and October to December.

Distribution and ecology. Known only from the frontier region of southern Ecuador with northern Peru, where it is confined to rocky riverbanks in lowland and montane rain forest, ascending to 1000 m altitude. It is resistant to periodic inundation during flash floods, and often present in dense stands.

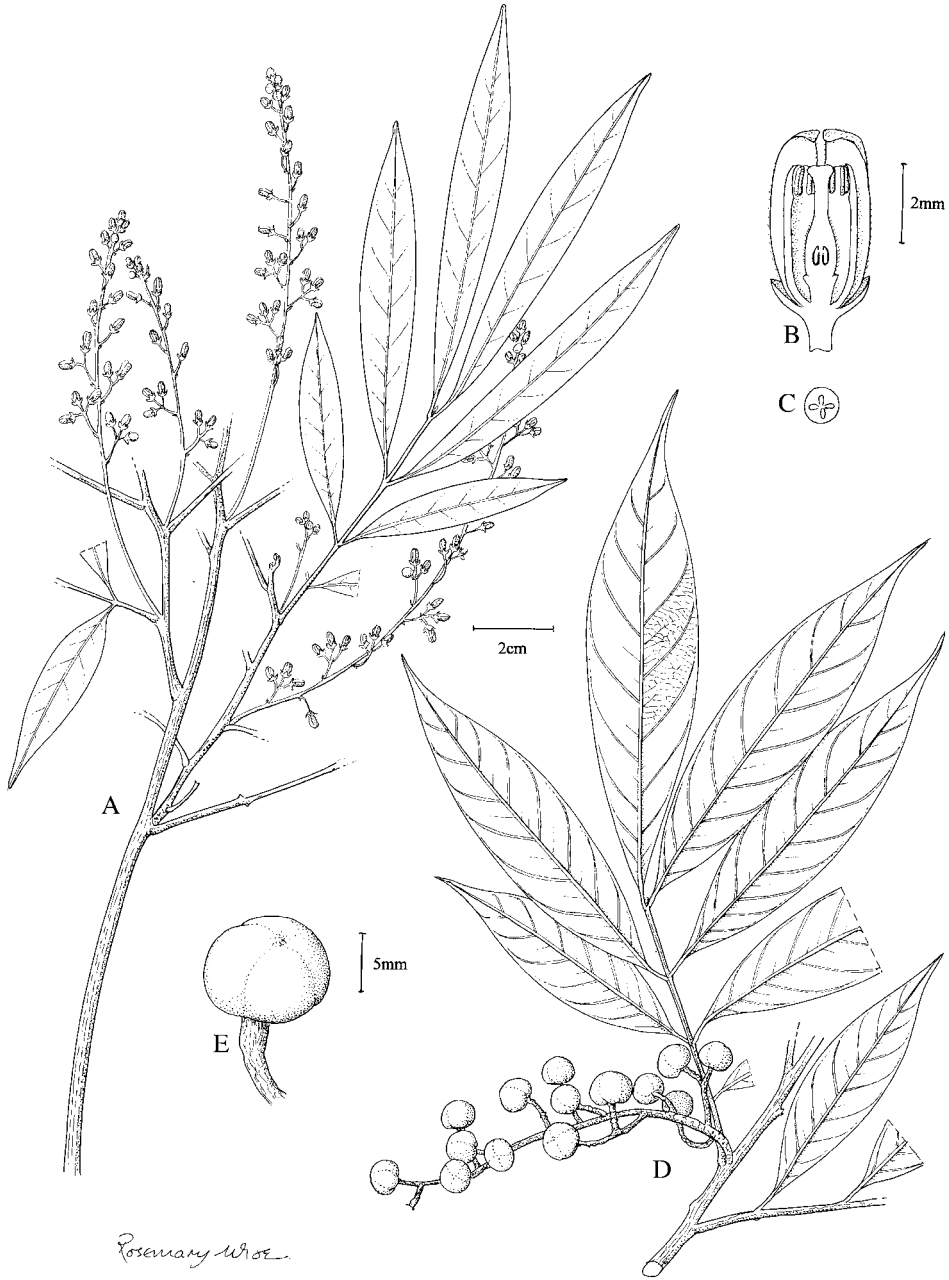


FIG. 30. *Guarea riparia* W. Palacios. A, habit; B, half-flower; C, cross-section of ovary; D, infructescence, E, fruit. (A-C, Palacios 8460; D, E, Vásquez et al. 19026).

Collections examined. ECUADOR. **Zamora-Chinchi**: Cantón Nangaritza, Destacamento Militar Shaima (SW0478), *Jaramillo* 13425 (NY), 14165 (MO, NY, QCNE); Rio Nangaritza, between Pachicutza and Miazi (SW0478), *Palacios* 6613 (K, MO), 6617 (K, QCNE), 8439 (K, MO), 8460 (QCNE).

PERU. **Amazonas**: 5 km N of confluence of Huampani and Cenepa (SW0478), *Berlin* 237 (F, MO); Rio Comaina, near Puesto Comando Chavez Valdivia (SW0478), *Ferreyra* 19471 (MO, US), 19474 (US); Condorcanqui Province Rio Comaina, between Cusu-Kubaim and Chavez Valdivia (SW0478), *Vásquez et al.* 19026 (K, QCNE); Distrito el Cenepa, Huampani, Suiva (SW0478), *Vásquez et al.* 22627 (F); Distrito el Cenepa, San Antonio (SW0478), *Vásquez et al.* 24055 (F).

The ITS phylogeny confirms the close morphological relationship of this species with *Guarea guidonia*, *G. persistens* and other small-flowered Amazonian species sharing a similar floral formula: 4 petals, 8 anthers, ovary 4-locular with 1-ovulate locules and small globose fruit. It differs from all these species in its slender narrowly elliptic leaflets which are 5–6 times as long as broad and in its unique ecology.

36. *Guarea pyriformis* T.D.Penn. in T.D.Penn. et al., *Fl. Neotrop.* 28: 278, fig. 56 (1981). – Type: Costa Rica, Puntarenas, Canton de Osa, near Palmar Norte de Osa, fl., *Allen* 5501 (holo K; iso A, F, G, NY, US). **Fig. 54C.**

Abbreviated description. Twigs often with pale, fissured, suberous bark, indumentum of young shoots and inflorescences pale yellowish tomentose or pubescent, persistent, leaves with indeterminate apical growth, with 2–7 pairs of leaflets, leaflets 14–20(–25) × 4–6.5(–7.5) cm, oblong, oblanceolate or narrowly elliptic, with some pubescence below, secondary veins 13–16 pairs, inflorescence ramiflorous, 4.5–17 cm long, a slender densely-flowered thyse, petals 4–5, valvate, 10–11 mm long, densely appressed pubescent or sericeous, staminal tube 8–8.5 mm long, 2.5–3 mm broad, anthers 9–10, ovary 4–5-locular, pubescent, locules 1-ovulate, capsule 2.3–3 cm long, shortly pyriform, 4–5-valved, smooth, minutely puberulous, pericarp 2–4 mm thick, valves 1-seeded.

Distribution and ecology. Pacific drainage of southern Costa Rica, Panama and western Colombia, where it is a tree of lowland rain forest, often along streams, up to 500 m altitude.

Additional collections examined. COSTA RICA. **Puntarenas**: Parque Nacional Manuel Antonio, Punta Catedral (NW0984), *Harmon* 33 (CR, K, MO).

PANAMA. **Panamá**: Llano–Carti road, 7 miles from Pan-Am highway (NW0979), *McPherson & Merello* 8204 (K); El Llano–Carti road, 12.7 km from Inter American highway (NW0979), *Mori & Kallunki* 4695 (K). **San Blas**: El Llano–Carti road, 16 km N of Panamerican highway (NW0979), *Folsom* 2619 (K, MO).

COLOMBIA. **Antioquia**: Municipio de San Carlos; ISH hydroelectric dam (NW0675), *McPherson* 13319 (MO); Rio Claro, Alto Rico (NW0575), *Renteria et al.* 2819 (MO); Municipio Anori, Valle del Rio Anori, between Dos Bocas and Anori (NW0775), *Soejarto et al.* 4134 (MO); San Carlos, El Jordan, embalse de Punchina-ISA (NW0674), *Velasquez et al.* 182 (MO). **Choco**: road to Lloro, 1–2 km SE of Yuto, 30 km S of Quibdo (NW0576), *Gentry & Renteria* 23803 (MO). **Valle**: Bajo Calima, road to Juanchaco Palmeras (NW0377), *Gentry et al.* 48283 (K); Bajo Calima, 15 km N of Buenaventura (NW0377), *Gentry et al.* 53691 (K, MO); Bajo Calima, Lijal-Gasolina road bifurcation (NW0377), *Gentry & Faber-Lagendoen* 62795 (K).

Although this species is not present in Amazonia, the ITS phylogeny and the morphology place it with species at the top of the Amazonian clade, close to *Guarea guidonia*, *G. persistens* and *G. gomma*. The flowers of all these species are morphologically very close, but *Guarea pyriformis* differs from them in the yellowish indumentum on the young shoots and in the fine detail of fruit structure.

37. *Guarea gomma* Pulle, Rec. Trav. Bot. Néerl. 6: 271 (1909); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 291, fig. 53 (1981). – Type: Surinam, Sectie O, fl., fr., *BW* 70 (holo U; iso K, NY). **Figs 31, 49D.**

Abbreviated description. Indumentum inconspicuous, puberulous, leaves without intermittent terminal growth, all leaflets opening \pm simultaneously, leaflets 6–10(–12) pairs, 14–30 \times 3–8.5 cm, narrowly oblong or oblanceolate (lower pairs often elliptic), with 12–18 pairs of secondary veins, subglabrous, often drying dark brown below, inflorescence 15–40 cm long, a slender, densely-flowered thyrses, petals 4–6, valvate, 8–12 mm long, staminal tube 6.5–8 mm long, 2–4 mm broad, anthers 8–10(–12), ovary 4–6(–7)-locular, locules with 1–2 superposed ovules, capsule 2.5–4 \times 2.5–3.5 cm, 4–6-valved, globose to shortly pyriform, smooth, densely papillose-puberulous, pericarp 2–4 mm thick, valves 1-seeded.

Distribution and ecology. Trans-Amazonian from southern Venezuela and the Guianas to Amazonian Colombia, Ecuador, Peru and Bolivia. It is a tree of non-flooded lowland and lower montane rain forest, altitudinal range up to 800 m.

Representative additional collections. GUYANA. Upper Essequibo Region, Rewa River, near Corona Falls (NW0358), *Jansen-Jacobs et al.* 5745 (K).

SURINAM. Tumuc Humac Mts., Talouakem (NW0254), *Acevedo-Rodríguez et al.* 6045 (K).

FRENCH GUIANA. Saül, Monts la Fumée (NW0353), *Boom & Mori* 2219 (K).

ECUADOR. **Napo:** Puerto Misahualli, Jatun Sacha Reserve (SW0177), *Zaruma* 791 (NY).

Orellana: Rio Tiputini, Yasuní Scientific Station (SW0076), *Villa et al.* 814 (US). **Pastaza:** Canton Pastaza, Pozo Petrolero ‘Danta 2’ de UNOCAL (SW0176), *Rubio & Coba* 790 (F). **Sucumbios:** Gonzalo Pizarro, Pto. Libre, Sinangue (NW0077), *Cerón & Montalvo* 20963 (K).

PERU. **Huánuco:** Puerto Inca, Yuyapichis, DANTAS (SW0975), *Tello* 2233 (K). **Loreto:** Yanamono Explorama Tourist Camp (SW0372), *Gentry et al.* 60922 (K).

BRAZIL. **Acre:** Município Sena Madureira (SW0968), *Daly et al.* 8197 (K).

BOLIVIA. **Pando:** Prov. Madre de Dios, Concesion de Mobil Oil (SW1267), *Killeen* 4464 (K).

38. *Guarea persistens* W.Palacios, Fl. Ecuador 82, Fam. 98, Meliaceae: 36, fig. 4 (2007). – Type: Ecuador, Napo, Canton Archidona, slopes of Volcán Sumaco, Hollin-Loreto road km 40 [SW0077], *Palacios & Iguago* 4561 (holo QCNE; iso MO). **Figs 32, 54D.**

Young shoots minutely appressed puberulous, soon glabrous, brown, smooth, with a few pale lenticels, twigs 6–10 mm diam., hollow. *Leaves* pinnate with a dormant, non-active, caducous terminal bud, petiole 14–22 cm long, semiterete, minutely appressed puberulous to glabrous, rhachis 10–38 cm long, semiterete, glabrous;

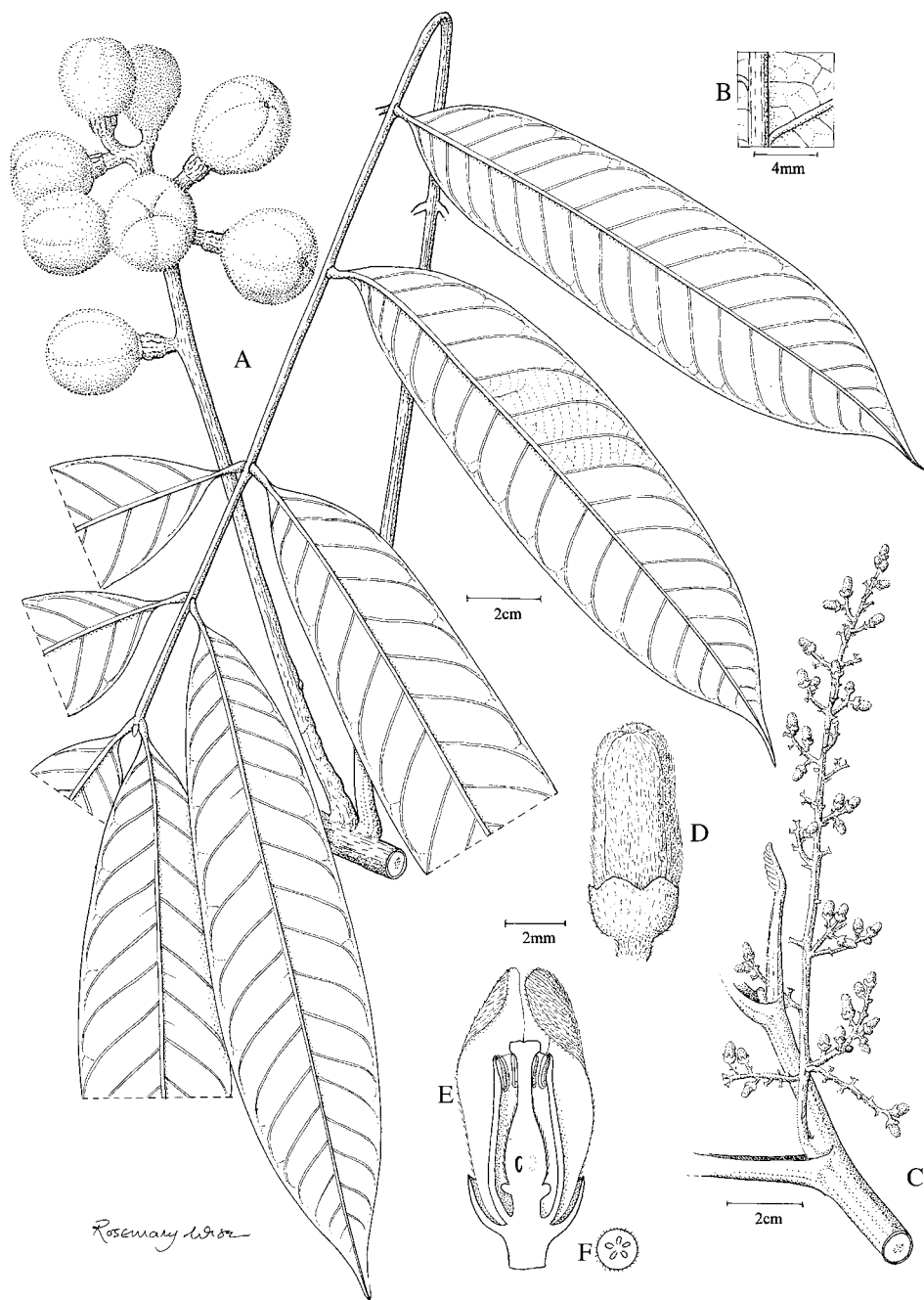


FIG. 31. *Guarea gomma* Pulle. A, habit; B, enlargement of leaf undersurface; C, inflorescence; D, flower bud; E, half-flower; F, cross-section of ovary. (A, B, *Jansen-Jacobs et al.* 5745; C-F, *Clarke, D.* 3625).

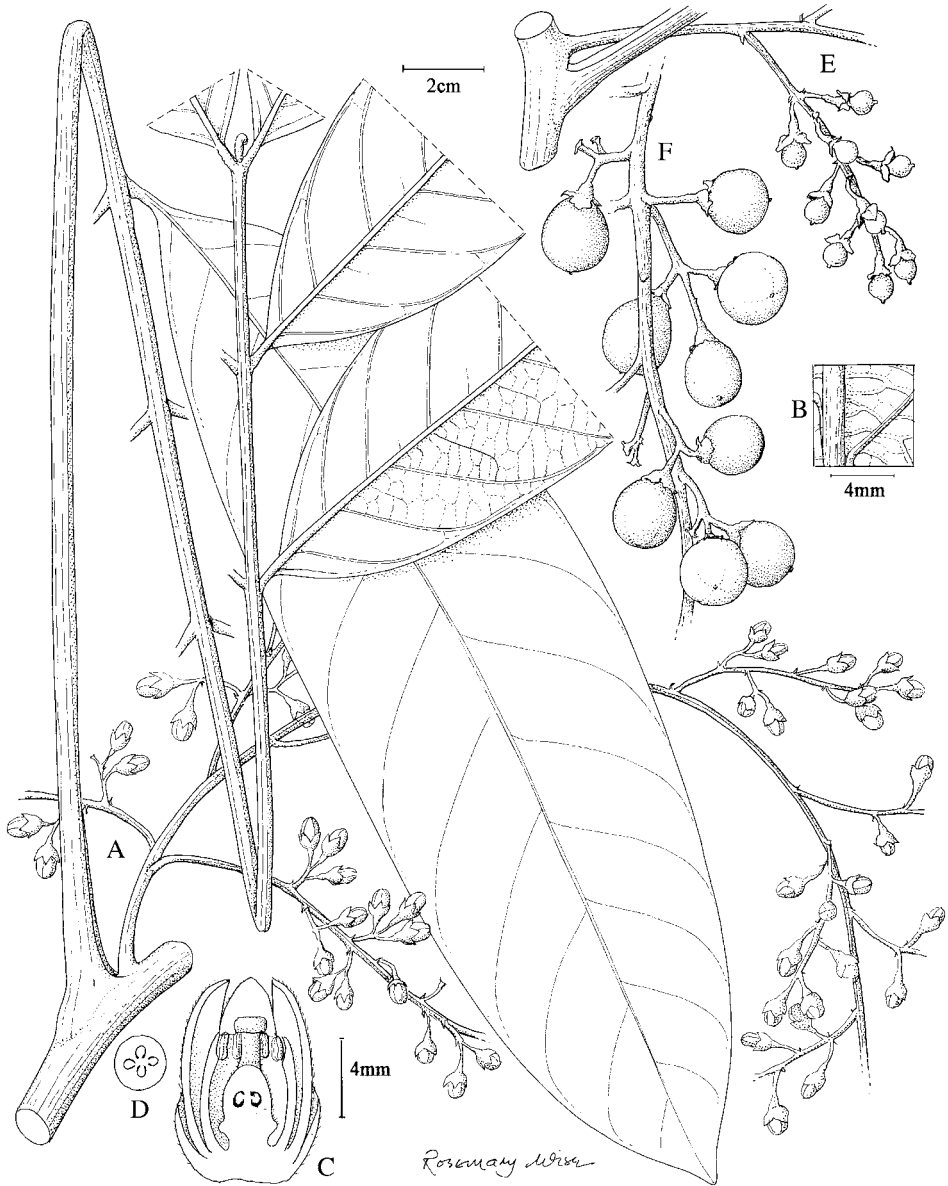


FIG. 32. *Guarea persistens* W. Palacios. A, habit; B, enlargement of leaf undersurface; C, half-flower; D, cross-section of ovary; E, young infructescence; F, infructescence. (A–D, Clark, *L.* 2298; E, Palacios 4665; F, Neill *et al.* 8602).

petiolule 5–10 mm long, swollen in the lower half, glabrous. *Leaflets* opposite, 5–8 pairs, 17.5–30.5 × 4.5–10.5 cm, elliptic, oblong or oblanceolate, apex narrowly acuminate to obtusely cuspidate, base narrowly attenuate to acute, thinly coriaceous,

glabrous, not glandular-punctate or -striate; venation eucamptodromous, midrib not raised or sunken on the upper surface, secondaries 11–12 pairs, steeply ascending, slightly arcuate and slightly convergent, intersecondaries absent, tertiaries oblique, obscure. *Inflorescence* axillary or on twigs below the leaves, 10–45 cm long, a laxly-branched, many-flowered panicle, lateral branches up to 20 cm long, finely puberulous; pedicel 5–6(–10) mm long (above the articulation). *Calyx* closed in bud, cup-shaped, 3–5 mm long, irregularly and deeply 3–4-lobed, lobes ovate, apex acute to obtuse, sparsely appressed puberulous outside; calyx usually persists in fruit. *Petals* 4–6, valvate, c. 9×2 –3 mm, narrowly triangular, acute, finely appressed puberulous outside, glabrous inside. *Staminal tube* 5–7 mm long, 2.5–3.5 mm broad, shortly tubular, margin undulate or truncate, glabrous; anthers 8–10, c. 1.2 mm long, glabrous; antherodes in female not dehiscent, without pollen. *Nectary* represented by a thick glabrous annulus beneath the ovary. *Ovary* 2–3 mm long, ovoid, 4(–5)-locular, locules 1-ovulate, finely appressed puberulous, style 2–3 mm long, subglabrous, style-head discoid. *Capsule* 1.7–2 cm long, shortly pyriform, apex truncate, base obtuse, 4-valved, smooth, finely appressed puberulous, pericarp c. 1 mm thick. *Seed* 1 in each valve, shaped like the segment of an orange, completely covered by a thin fleshy sarcotesta.

Field characters. Treelet or small tree to 10 m high and 15 cm diam., with hollow twigs inhabited by ants, and flowers with a reddish corolla. The purple or reddish fruit are held in large many-fruited pendulous clusters, and the seed is surrounded by a bright red sarcotesta. Most flowering occurs in March and April, with the fruit maturing September to October.

Distribution and ecology. Amazonian slopes of the Andes in Ecuador in wet montane rain forest from 650 m to 1300 m altitude.

Specimens examined. ECUADOR. **Napo:** Cantón Archidona, slopes of Volcán Sumaco, Hollin-Loreto road, km 40 (SW0077), *Alvarado* 38 (K); Parque Nacional Sumaco, Pacto Sumaco (SW0077), *Alvarez et al.* 1866 (K, NY); Sumaco Napo-Galeras National Park, Pacto Sumaco to Loreto road (SW0077), *J.L. Clark* 2298 (K, MO, QCNE); Hollin-Loreto, Caserío de Huamani (SW0077), *Palacios* 4661 (K, MO, NY, QCNE); Cantón El Chaco, Rio Granadillo (SW0077), *Palacios* 5543 (MO, QCNE); Cantón El Chaco, Codo Sinclair (SW0077), *Palacios* 5665 (MO, QCNE), 5750 (MO), 5754 (MO), 5768 (MO), 5774 (QCNE); Faldas Sur del Volcán Sumaco, Challua (SW0077), *Palacios & Iguago* 4557 (MO, QCNE); Faldas Sur del Volcán Sumaco, Hollin-Loreto km 40 (SW0077), *Tipaz et al.* 378 (MO).

Guarea persistens is morphologically close to *G. fissicalyx*, which has a similar vegetative and floral structure. It differs in its hollow twigs (said to be inhabited by ants), in its laxly-branched inflorescence with long lateral branches, in the flowers borne on long slender pedicels, in the calyx which persists in the developing fruit and in the 4-locular ovary. The ecology of the species also differs, with *Guarea persistens* occurring in lower montane forest, while *G. fissicalyx* is confined to riverbanks and periodically flooded lowland forest. The ITS phylogeny confirms their close relationship near the top of the Amazonian clade.

39. *Guarea purusana* C.DC., Bull. Herb. Boissier, Sér. 2, 6: 984 (1906); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 355, fig. 75 (1981). – Type: Brazil, Amazonas, Alto Purus, fr., *Huber* 4394 (lecto G, designated by Pennington in Pennington et al. (1981: 355); isolecto INPA, MG, RB). **Fig. 49E.**

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 355 (1981).

Abbreviated description. Young shoots and inflorescences coarsely pubescent with dark brown hairs, leaves with a terminal bud showing intermittent growth, leaflets 4–7 pairs, 18–34 × 5–9.5 cm, oblong or narrowly oblanceolate, chartaceous to thinly coriaceous, upper surface subglabrous, lower surface with indumentum on midrib and veins, secondary veins 17–24 pairs, usually straight and parallel, inflorescence axillary or in the axils of fallen leaves, 5–30 cm long, a slender densely-flowered panicle with short lateral branches to 2 cm long, petals 4–5, valvate, 9.5–10.5 mm long, appressed pubescent or sericeous outside, staminal tube 7.5–8 mm long, 2–3 mm broad, anthers 8–11, ovary 5–8-locular, locules with (1–)2 superposed ovules, capsule 3.5–5.2 × 2.2–3 cm, obovoid to shortly botuliform, smooth or slightly constricted between the valves, minutely papillose, 5–8-valved, valves with 2 superposed seeds, pericarp 4–6 mm thick.

Distribution and ecology. Transamazonian from the mouth of the Amazon to southern Venezuela, Amazonian Brazil, Colombia, Ecuador, Peru and Bolivia. Apparently not present in the Guianas. In lowland rain forest, equally common on non-flooded land and in periodically flooded forest.

Representative additional collections. COLOMBIA. **Amazonas:** Rio Caquetá, Isla Mariname (NW0172), *Urrego* 544 (NY).

VENEZUELA. **Territorio Federal Amazonas:** Dep. Atabapo, la base de Cuerpo Circular (NW0263), *Marín* 1764 (K, MO).

ECUADOR. **Napo:** Jatun Sacha Biological Station (SW0177), *Palacios & Freire* 5150 (K). **Orellana:** La Joya de los Sachas, Cantón Pompeya (SW0076), *Gudiño & Greff* 1818 (K). **Pastaza:** Cantón Pastaza, Pozo Petrolero 'DANTA 2' (SW0176), *Espinoza & Coba* 446 (K). **Sucumbios:** Lumbaqui (NW0077), *Pennington et al.* 12293 (K).

PERU. **Amazonas:** Dist. Imaza, Yamayakat (SW0578), *Vásquez & Vásquez* 21031 (F). **Huánuco:** Prov. Puerto Inca, Llullapichis, DANTAS (SW0975), *Palomares* 9 (K). **Loreto:** Maynas, Rio Napo, Sucursari (SW0372), *Gentry et al.* 42681 (K).

BRAZIL. **Acre:** Fazenda Bom Sossego (SW0773), *Campbell et al.* 8836 (K). **Amazonas:** Municipio de Borba, BR 230 Transamazonica (SW0659), *Henderson et al.* 398 (K). **Pará:** Cuanta do Anajas (SW0049), *Prance et al.* 30291 (K).

BOLIVIA. **Beni:** Ballivian Prov., km 35 Yacumo – Rurrenabaque (SW1467), *D.N. Smith et al.* 14361 (K). **Pando:** 54 km SW of Cobija, Triunfo (SW1169), *R.T. Pennington et al.* 13 (K).

This species is both morphologically and phylogenetically close to *Guarea grandifolia*. It differs from *Guarea grandifolia* in the rather narrow oblong or oblanceolate leaves with numerous parallel secondary veins, and in the size and fine detail of the fruit.

40. *Guarea guidonia* (L.) Sleumer, Taxon 5: 194 (1956); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 261 (1981). – *Samyda guidonia* L., Sp. Pl. ed. 1, 443 (1753). – Type: Illustration of *Samyda foliis ovatis acuminatis* in Plumier in Burman, Pl. Amer. 139, t. 147, f. 2 (1757), designated by Pennington in Pennington *et al.* (1981: 265). **Figs 33, 65A.**

Guarea brachystachya DC., Prodr. 1: 624 (1824). – Lectotype (icon): Torner Collection plate no. 1478, chosen by McVaugh (2000).

For further synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 261–263 (1981).

Abbreviated description. Indumentum inconspicuous, puberulous to pubescent, leaves with indeterminate apical growth, leaflets up to 9(–14) pairs, (6.5–)10–16(–25) × (2.5–)3–6(–9) cm, elliptic, oblong, lanceolate or oblanceolate, glabrous, secondary veins (6–)9–12(–17) pairs, inflorescence (4–)10–25(–45) cm long, a pyramidal thyrse, petals (3–)4–5, valvate, (5–)5.5–7.5(–9.5) mm long, staminal tube 3.5–7 mm long, (1–)1.5–2.5(–3) mm broad, anthers (7–)8(–11), ovary (3–)4(–5)-locular, locules 1-ovulate, pubescent, capsule 1.5–2.5 cm long, globose to fig-shaped, 4-valved, usually with short stipe at base, pericarp smooth, not wrinkling on drying, shining, usually with conspicuous pale lenticels, glabrous, pericarp 1–2 mm thick, valves 1-seeded.

Distribution and ecology. Nicaragua, Costa Rica and Panama and throughout tropical America to Paraguay and northern Argentina, also in the Greater Antilles. In much of Amazonia it is a common tree of riverbanks and periodically flooded forest, but in the western Amazonian part of its range and in the Caribbean it is frequently found in non-flooded forest.

Representative additional collections. COSTA RICA. **Alajuela:** San Carlos, Fortuna RB, Arenal Mundo Aventura (NW1084), *Rodríguez* 8481 (INB). **Heredia:** Sarapiquí, ZP la Selva (NW1084), *Kriebel et al.* 4019 (INB). **Limón:** Cantón Pococi, RNFS Barra del Colorado, Sardinias (NW1083), *Araya* 39 (INB). **Puntarenas:** Osa, Cuenca Terraba-Sierpe (NW0883), *Gonzalez* 3621 (INB).

CUBA. **Camaguey:** NE Sierra de Cubitas, Los Paredones (NW2177), *Rico et al.* 2022 (K).

PUERTO RICO. Caribbean National Forest, El Verde Research Station (NW1865), *Boom* 10231 (K).

VENEZUELA. **Anzoategui:** Distrito Libertad, road from El Vigia to Buenos Aires (NW1064), *Davidse & Gonzalez* 19481 (MO). **Barinas:** Distrito Pedraza, Curbati to El Algarrobo (NW0870), *Dorr et al.* 4695 (K). **Bolívar:** Municipio Sucre, Rio Caura, below Salto Aimara (NW0463), *Elcoro* 77 (K). **Carabobo:** 5 km N of Bejuma, Hacienda La Calceta (NW1068), *Meier* 3120 (K).

GUYANA. Potaro-Siparuni region, 4–5 km N of Surama (NW0459), *Hoffman et al.* 1526 (K).

SURINAM. Tumuc Humac Mts., Talouakem, upper Litani River (NW0254), *Acevedo-Rodríguez et al.* 5817 (K).

FRENCH GUIANA. Inini (NW0353), *Fleury* 841 (K).

ECUADOR. **Morona-Santiago:** Sucua (SW0278), *Pabón et al.* 296 (K). **Napo:** Jatun Sacha Biological Station (SW0177), *Cerón & Cerón* 1300 (K). **Orellana:** Rio Napo, 5 km below Coca (SW0076), *Neill et al.* 6901 (K). **Zamora-Chinchipec:** 17 km NE of Zamora (SW0478), *Pennington & Tenorio* 10738 (K).

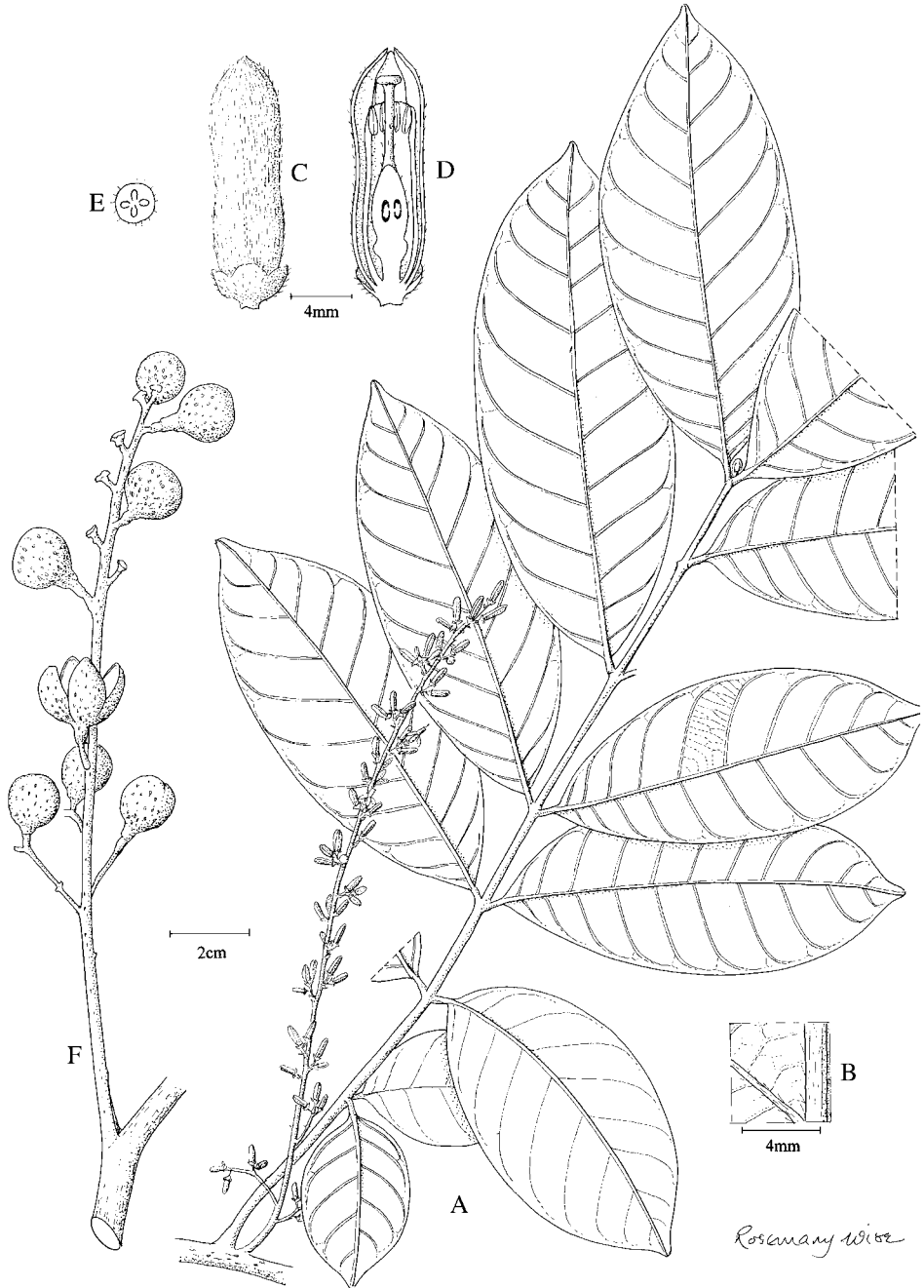


FIG. 33. *Guarea guidonia* (L.) Sleumer. A, habit; B, enlargement of leaf undersurface; C, flower; D, half-flower; E, cross-section of ovary; F, infructescence. (A–E, Hahn & Tiwari 5213; F, Hoffman *et al.* 1526).

PERU. **Junín**: San Ramón, Catarata del Tirol (SW1175), *Daza et al.* 16282 (K). **Loreto**: Requena, Yanallpa, R. Ucayali (SW0473), *de Jong* 177 (K).

BRAZIL. **Acre**: Municipio Tarauaca, Rio Muru, Seringal Vitoria Velha (SW0870), *Figueiredo et al.* 955 (K). **Bahía**: Municipio Jacobina, Chapada Diamantina (SW1140), *Stannard et al.* 2617 (K). **Distrito Federal**: APA de Cafuringa (SW1547), *Pereira & Alvarenga* 2216 (K). **Espírito Santo**: Municipio Piuma, road to Itapemirím (SW2040), *Pirani et al.* 4745 (K). **Goias**: Municipio de Cabeceiras de Goias, km 15, on BR-020 (SW1547), *Pereira & Alvarenga* 3052 (K). **Mato Grosso**: Serra das Araras, Vale de Currupira (SW1556), *Dubs* 2000 (K). **Mato Grosso do Sul**: Municipio Bodoquena, km 6 road to Bonito (SW2056), *Pirani et al.* 4851 (K). **Minas Gerais**: Caratinga (SW1942), *Braga et al.* 19526 (K). **São Paulo**: Municipio Teodoro Sampaio, Reserva Florestal Morro do Diabolo (SW2252), *Pastore & Klein* 59 (K).

BOLIVIA. **La Paz**: Prov. Nor Yungas, Alto Beni, Puerto Carmen, *Seidel et al.* 7570 (K). **Santa Cruz**: Prov. Ichilo, 1 km S of Carandá (SW1763), *Saldias & Lawrence* 1435 (K).

PARAGUAY. **Amambay**: Cerro Lorito, Estância la Serrana (SW2255), *Zardini & Cardozo* 45094 (K).

Guarea brachystachya DC. is based on an illustration made for Sesse & Mocino's unpublished 'Flora Mexicana'. The original illustrations were loaned to de Candolle at Montpellier in France, where he was preparing the Prodrômus, and he arranged for rough tracings to be made of them before returning the originals to Barcelona in 1820. The drawings were then lost for 150 years. The tracings made by de Candolle, known as the 'Calques des dessins', were often the sole basis of some species in the Prodrômus, including no. 155 which is *Guarea brachystachya*. This was chosen as the lectotype of the species in *Flora Neotropica* (Pennington *et al.*, 1981). However, the original drawings were rediscovered in Spain in 1979, and they were acquired by the Hunt Institute for Botanical Documentation Library, where they are now known as the Torner Collection.

McVaugh (2000) pointed out that a better choice, as lectotype, would have been plate no. 1478 in the Torner Collection, from which DC. Plate 155 was copied. Torner 1478, which we have now had an opportunity to study, is annotated '*Guarea brachystachya*' by A. P. de Candolle. On the basis of DC. Plate 155 this species was placed in the synonymy of *Guarea glabra* by Pennington in Pennington *et al.* (1981), but after examining the much more detailed Torner 1478, we consider that it should be in the synonymy of *G. guidonia*. The stout, many-flowered inflorescence and lenticellate twigs and fruit all point to *Guarea guidonia*. It is not known for certain whether the drawing was made in Cuba or Puerto Rico, but *Guarea glabra* is absent from Cuba, and in Puerto Rico is characterised by a very short, few-flowered inflorescence, and the fruits and twigs are not lenticellate.

41. *Guarea fissicalyx* Harms, Notizbl. Bot. Gart. Berlin-Dahlem 11: 383 (1932); Palacios, Fl. Ecuador 82, Fam. 98, Meliaceae: 24 (2007). – Type: Peru, Loreto, Florida [SW0174], fl., *Klug* 2090 (holo B, destroyed; lecto K, designated here; isolecto F, GH, MO, NY, S). **Figs 34, 54E.**

Guarea gomma auct. non Pulle: T.D.Penn. in T.D.Penn. *et al.*, Fl. Neotrop. 28: 291 (1981), p.p.

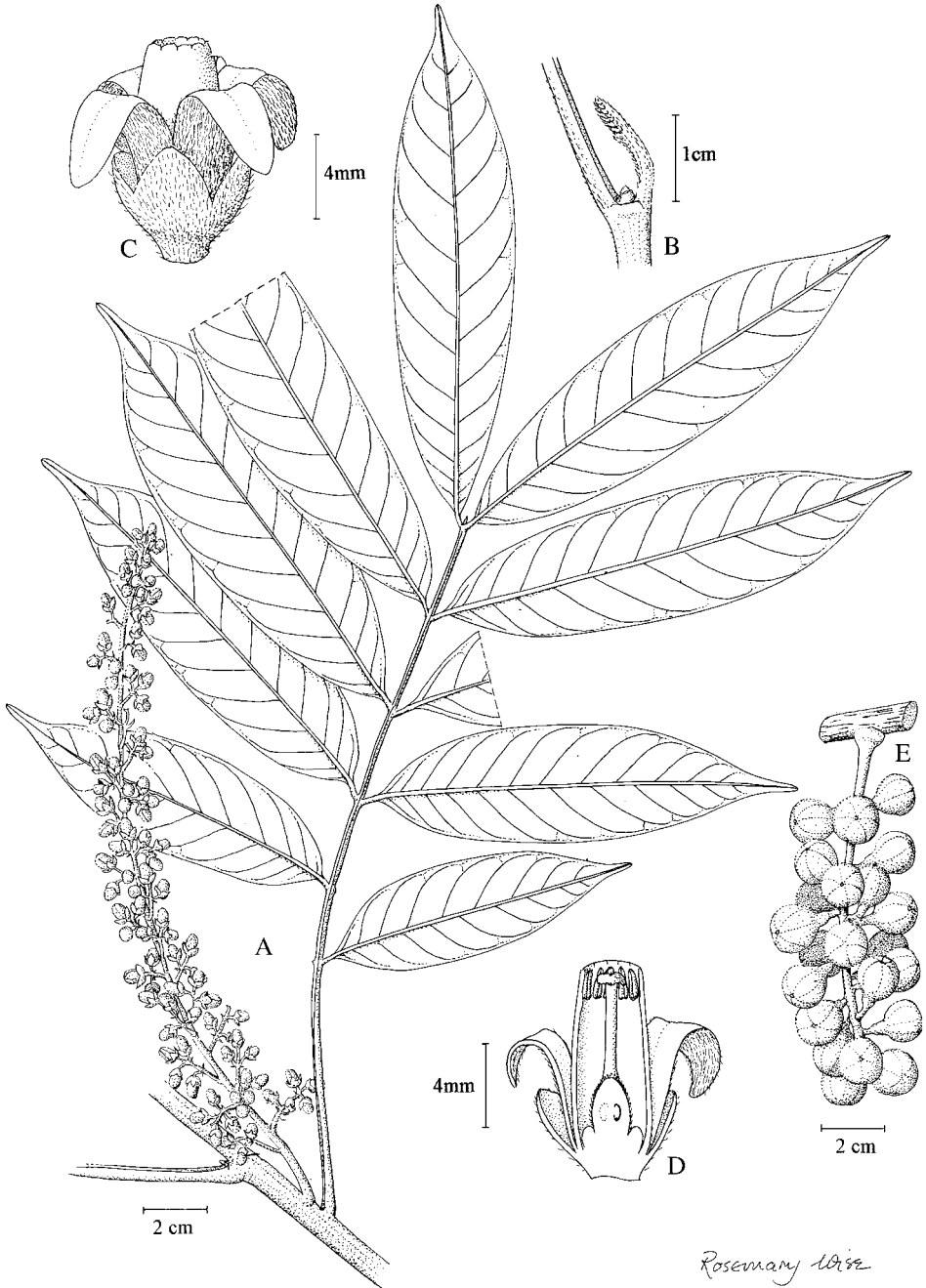


FIG. 34. *Guarea fissicalyx* Harms. A, habit; B, shoot apex; C, flower; D, half-flower; E, infructescence. (A, B, Schultes 46-303; C, D, Vásquez & Jaramillo 6333; E, Zarucchi & Balick 1768).

Young shoots 5–8 mm diam., usually solid, minutely appressed puberulous, soon glabrous, pale greyish-brown, smooth, without lenticels. *Leaves* pinnate with a caducous terminal bud, without intermittent growth, petiole 6.5–13 cm long, semiterete to terete at the apex, finely appressed puberulous to glabrous, rhachis 16–40 cm long, semiterete, subglabrous; petiolule 2–8 mm long, glabrous. *Leaflets* opposite, 4–8 pairs, 12–22 × 3–6 cm, usually elliptic, elliptic-lanceolate or oblanceolate, occasionally oblong, apex narrowly attenuate or acuminate, base usually obtuse or rounded, occasionally narrowly cuneate, thinly coriaceous, glabrous or with sparse pubescence on lower midrib, not glandular-punctate or -striate; venation eucamptodromous, midrib sunken on the upper surface, secondaries 10–12(–14) pairs, ascending, straight or slightly arcuate, slightly convergent, intersecondaries absent, tertiaries oblique. *Inflorescence* axillary or on twigs below the leaves, 10–40 cm long, a slender many-flowered thyrse with lateral branches 1–3 cm long, puberulous; pedicel c.1 mm long (above the articulation). *Calyx* closed in bud, 3–4 mm long, cup-shaped, deeply and irregularly 3–4-lobed to halfway or more, sometimes to near the base, the lobes obtuse to rounded, sparsely puberulous on both surfaces. *Petals* 5–6, valvate, 7–8 mm long, 1.5–3 mm broad, strap-shaped, apex acute, densely appressed puberulous outside with pale yellowish hairs, glabrous inside. *Staminal tube* c.6 mm long, 2–3 mm broad, margin undulate, glabrous; anthers 9–11, c.1 mm long, oblong, glabrous. *Nectary* a broad stipe c.1 mm long surmounted by a narrow collar, glabrous. *Ovary* pubescent, 5–6-locular, locules with 1 ovule, style stout, c.4 mm long, with a broad discoid style-head. *Capsule* 1.5–2.2 cm long, broadly pyriform, apex truncate, sometimes tapering to a short stipe at the base, 4–6-valved, smooth, glabrous, pericarp 0.5–1 mm thick, valves 1-seeded. *Seeds* c.1 cm long, shaped like the segments of an orange, thin-walled.

Field characters. Tree to 25 m high and 50 cm diam., flowers with reddish calyx and cream-coloured corolla; the calyx is completely closed in bud and splits irregularly. Flowering is recorded from March to May and in November, fruiting in April.

Distribution and ecology. Amazonian Colombia, Ecuador and Peru, usually along riversides and in periodically flooded forest.

Collections examined. COLOMBIA. **Amazonas:** Rio Loretoyacu (SW0370), *Black & Schultes* 46-303 (K). **Vaupés:** Mitú (NW0170), *Zarucchi & Balick* 1768 (K).

ECUADOR. **Sucumbios:** Cuyabeno Reserve, from outlet of Laguna Grande and 5 km upstream (NW0076), *Balslev et al.* 84780 (MO); Cantón Lago Agrio, Cuyabeno Reserve, banks of R. Aguatico (SW0075), *Palacios et al.* 9466 (K, MO, NY, QCNE); Cuyabeno Reserve, Zancudo (SW0075), *Palacios et al.* 8161 (QCNE).

PERU. **Loreto:** Centro de Investigaciones de Jenaro Herrera (SW0473), *Collector unknown*, tree no. 7-3/8 (K, MOL); Jenaro Herrera, Supay Cocha, Quebrada Braga (SW0473), *Daly et al.* 5770 (K); *Freitas* 78 (K); Maynas, Sargento Lores, below Tamishiyacu (SW0472), *McDaniel & Rimachi* 23667 (K); Requena, Jenaro Herrera, Bosque Ribereño 'Braga' (SW0473), *Valcarcel* 525 (K); Maynas, Progreso (Isla Iquitos) (SW0373), *Vásquez & Jaramillo* 6274 (K); Maynas, Yanamono, Campamento Explorama Lodge (SW0372), *Vásquez & Jaramillo* 6329 (K), 6333 (K); Requena, Sapuena, Jenaro Herrera (SW0473), *Vásquez & Jaramillo* 10108 (K, NY).

This species was treated by Pennington in Pennington *et al.* (1981) as a doubtful synonym of *Guarea gomma*, but was recently reinstated by Palacios (2007). Additional, complete material has clarified and confirmed the differences between the species, which although they are slight and break down individually, in combination provide a discontinuity. They are enumerated below.

Guarea gomma: leaflets oblong, secondary veins 12–18 pairs, calyx shallowly to deeply regularly divided, petals 8–12 mm long, fruit 2.5–4 cm long.

Guarea fissicalyx: leaflets usually elliptic, secondary veins 10–12(–14) pairs, calyx deeply and irregularly divided, petals 7–8 mm long, fruit 1.5–2.2 cm long.

Guarea fissicalyx is nearly always recorded from riversides or periodically flooded forest, whereas *G. gomma* occurs in non-flooded forest.

42. *Guarea grandifolia* DC., Prodr. 1: 624 (1824); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 336 (1981). – Type: French Guiana specimen annotated ‘Cayenne ou Guyane-francoise, Museum de Paris 1821’, fl., *Collector unknown* s.n. (holo G-DC). **Figs 35, 65B.**

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 336 (1981).

Abbreviated description. Indumentum of young shoots and inflorescence variable, from puberulous to tomentose, leaves with a terminal bud showing intermittent growth, leaflets up to 10(–22) pairs, 13.5–37(–63) × (3.4–)4.5–13(–20) cm, oblong or elliptic, less frequently oblanceolate, chartaceous to coriaceous, glabrous above, veins puberulous to tomentose below, lamina sparsely puberulous or pubescent, or glabrous, inflorescence axillary or ramiflorous, rarely cauliflorous, 10–40(–50) cm long, a pyramidal thyse, petals 4–5(–7), valvate, (9–)10–14(–17) mm long, staminal tube (7–)9–11(–14) mm long, (2–)3–5 mm broad, anthers (8–)10–12(–13), ovary (4–)7–8(–10)-locular, locules with 2 superposed ovules, capsule 3.5–6(–8) cm long, 3–4(–7) cm broad, globose, ellipsoid, pyriform or obovoid, often tapering for 2/3 of its length to a short stout stipe, smooth or faintly longitudinally lined, densely puberulous or papillose, 5–8-valved, valves with 2 superposed seeds, pericarp 5–6(–15) mm thick.

Distribution and ecology. Southeastern Mexico, throughout Central America and northern and western South America. A tree of non-flooded lowland rain forest, in Central America often recorded from riverbanks.

Representative additional collections. MEXICO. **Chiapas:** Huehuetán, Belisario Dominguez (NW1592), *Ventura & Lopez* 220 (NY). **Veracruz:** San Andres Tuxtla, Los Tuxtlas Biological Station (NW1895), *Ibarra & Sinaca* 1966 (MEXU, NY).

GUATEMALA. **Izabal:** Santo Tomas de Castilla (NW1588), *Marshall et al.* 386 (K).

BELIZE. **Toledo:** Southern Maya Mountains, Bladen Nature Reserve (NW1688), *Davidse & Holland* 36491 (K).

HONDURAS. **Atlántida:** N slope of Pico Bonito, Campamento Quebrada Grande (NW1586), *Liesner & Mexia* 26038 (K). **Gracias a Díos:** R. Mocerón (NW1584), *Nelson & Vargas* 5087 (K). **Yoro:** E of San José Texiguat (NW1587), *Brant & Hazlett* 2881 (K).

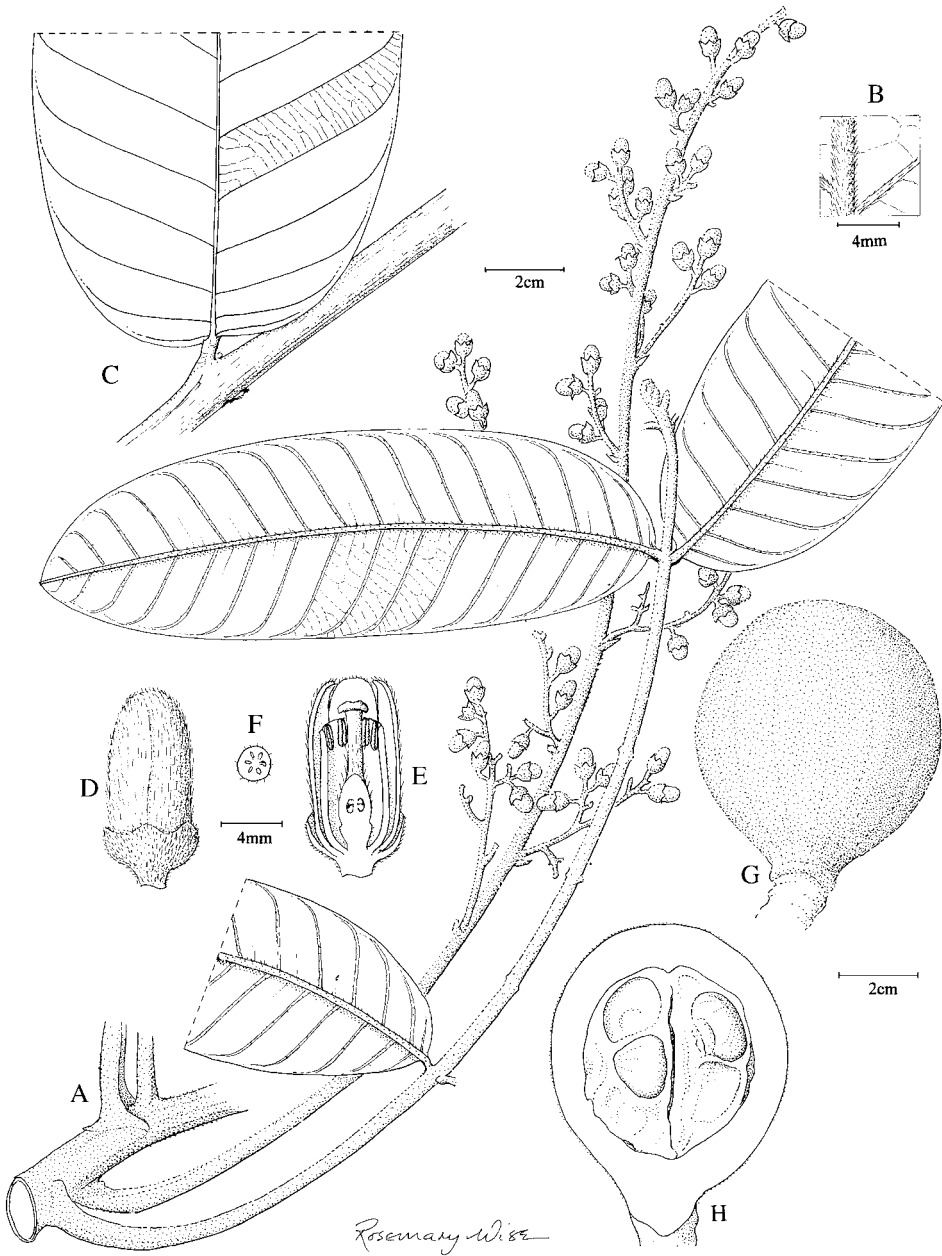


FIG. 35. *Guarea grandifolia* DC. A, habit; B, enlargement of leaf undersurface; C, base of mature leaflet; D, flower bud; E, half-flower; F, cross-section of ovary; G, fruit; H, longitudinal section of fruit. (A, B, *Lanjouw* 836; C-F, *Mori et al.* 22645; G, H, *Mori et al.* 15685).

NICARAGUA. **Boaco**: Cerro Mombachito (NW1285), *Stevens & Hahn* 18932 (K). **Chontales**: between Rio Rizcocho & Rio El Jordan (NW1285), *Stevens & Montiel* 21471 (K). **Zelaya**: Neptune Mining Co. (NW1484), *Pipoly* 3515 (NY).

COSTA RICA. **Alajuela**: Monteverde Reserve, Río Peñas Blancas (NW1084), *Bello* 606 (K). **Heredia**: Puerto Viejo de Sarapiquí (NW1084), *Hammel & Grayum* 17333 (K). **Puntarenas**: Corcovado National Park, Skyway trail (NW0883), *Kernan & Phillips* 687 (K). **San José**: Cantón Puriscal, Cuenca del Pirris-Damas (NW0984), *Jimenez & Acosta* 2261 (INB).

PANAMA. **Darien**: western slope of Serrania de Pirre, below Cana mine (NW0777), *McPherson* 12270 (MO). **San Blas**: Cangandi (NW0979), *Nevers & Herrera* 7096 (K).

COLOMBIA. **Amazonas**: Araraquara, R. Caquetá (SW0072), *Alvarez et al.* 670 (K). **Antioquia**: Municipio Mutata, Sabaletas (NW0776), *Callejas et al.* 9765 (K).

VENEZUELA. **Amazonas**: Rio Metacuni, Frente No. 4, *Stergios & Velazco* 14223 (K).

GUYANA. Upper Essequibo Region, Rewa River, Corona Falls (NW0358), *Jansen-Jacobs et al.* 5782 (K, NY, U).

SURINAM. Kabelebo Dam area, Nickerie Dist. (NW0457), *Lindeman & de Roon* 890 (K).

FRENCH GUIANA. Montagne Bellevue de l'Inini (NW0353), *de Granville et al.* 7628 (K, NY).

ECUADOR. **Orellana**: Orellana, Huaorani Reserve, Miwaguino (SW0076), *Freire & Naranjo* 681 (K). **Sucumbios**: Shushufindi, El Pilchi (SW0076), *Freire & Chavez* 5420 (K). **Zamora-Chinchipe**: Nangaritza, Cordillera del Condor, R. Numpatakaime (SW0478), *Quizhpe et al.* 500 (K).

PERU. **Amazonas**: Bagua Province, Dist. Imaza, Yamayakat (SW0478), *Jaramillo et al.* 167 (K). **Loreto**: Yanomono Explorama Tourist Camp, Rio Amazonas (SW0372), *Gentry et al.* 36565 (K).

BRAZIL. **Acre**: Fazenda Bom Sossego, between Igarapé do Cujubim & Jacamín (SW0773), *Campbell et al.* 9034 (K). **Amazonas**: Municipio São Paulo de Olivença, 8 km S (SW0368), *Daly et al.* 4489 (K). **Roraima**: Yanomami Indigenous area, near Xitei mission (NW0263), *Milliken* 2336 (K).

43. Guarea agularii Al.Rodr., Lankesteriana 6: 103 (2006). – Type: Costa Rica, Puntarenas, Parque Nacional Corcovado, Llorona to Los Planes [NW0883], *Kernan & Phillips* 1020 (holo INB). **Fig. 60A.**

Young shoots stout, 1–1.5 cm diam., minutely appressed puberulous at first, becoming glabrous, smooth, brown, with some long pale lenticels. *Leaves* pinnate with an active terminal bud, petiole 9.5–12.5 cm long, semiterete, subglabrous, rhachis up to 40 cm long, semiterete to slightly channelled, subglabrous; petiolule swollen, 0.5–1 cm long. *Leaflets* opposite, up to 4 pairs, 25–40 × 10–15 cm, broadly elliptic to oblong-elliptic, apex acuminate, base acute to narrowly cuneate, chartaceous, glabrous; venation eucamptodromous, midrib sunken on the upper surface, secondaries 14–15 pairs, ascending, straight, parallel, intersecondaries absent, tertiaries oblique. *Inflorescence* ramiflorous or cauliflorous, a small panicle up to 8 cm long, lateral branches to 3 cm long, pedicel 1–2 mm long above the articulation. *Calyx* 5–6 mm long, margin shallowly lobed, minutely puberulous. *Petals* 5–6, 15–16 mm long, 1.5–2 mm broad, apex acute, sericeous outside, glabrous inside. *Staminal tube* 11–12 mm long, c.4 mm broad, margin shallowly toothed, glabrous; anthers 12, 2–2.5 mm long. *Nectary* 2–2.5 mm long, expanded below the ovary. *Ovary* 6–9-locular, locules with 2 superposed ovules, sericeous, style glabrous, style-head discoid. *Fruit* 3–5 cm long, depressed-globose and

slightly broader than long, depressed at the apex, base truncate, 6–9-valved, strongly constricted between the valves when dry, glabrous with pale lenticels.

Field characters. Tree to 30 m high and 25 cm diam., flowers cream-coloured, fruit maturing orange to red, the seed covered by an orange arillode. Flowering recorded in September, fruiting in March, April and September.

Distribution and ecology. Pacific slopes of Costa Rica (Puntarenas and San José), in wet forest up to 700 m altitude.

Collections examined. COSTA RICA. **Puntarenas:** Osa, Osa Peninsula, Aguabuena (NW0883), Aguilar 476 (INB); Osa, near Rincón, Rancho Quemado (NW0883), Gentry *et al.* 78671 (INB); Fila Estero Guerra, Sierpe (NW0883), Marin 217 (INB). **San José:** Tarrazu, San Lorenzo, E of R. Naranjo (NW1084), Sanchez *et al.* 748 (CR).

This plant is morphologically very close to *Guarea grandifolia* except that the capsule is unusually constricted between the valves. All other characters of leaves and flowers fall easily within the variation of *Guarea grandifolia*.

44. *Guarea cartaguenya* Cuatrec., Fieldiana, Bot. 27(1): 70 (1950); T.D.Penn. in T.D.Penn. *et al.*, Fl. Neotrop. 28: 345, fig. 75 (1981). – Type: Colombia, Dept. del Valle, Cordillera Occidental, Hoya del Rio Anchicaya, fr., *Cuatrecasas* 15218 (holo F; iso COL). **Fig. 55A.**

Abbreviated description. Young shoots and inflorescences puberulous, leaves with a terminal bud showing intermittent growth, leaflets up to 8 pairs, 22.5–40 × 7.5–14.5 cm, oblong, elliptic or oblanceolate, glabrous above, crisped puberulous below with pale hairs, eventually becoming glabrous, coriaceous, inflorescence axillary, 35–50 cm long, a broad and laxly-branched pyramidal panicle, lower branches up to 26 cm long, petals 4–5, 15–17.5 mm long, appressed puberulous to finely sericeous outside, staminal tube 12–13 mm long, 4–5 mm broad, anthers (9–)10–12, ovary 4–6(–7)-locular, locules with 2 superposed ovules, capsule 6–9 cm long, 5–7 cm broad, obovoid to pyriform, faintly longitudinally ribbed when dry, otherwise smooth, finely puberulous or papillose, 5–6-valved, pericarp 5–10 mm thick, valves with 2 superposed seeds.

Distribution and ecology. Pacific drainage of Colombia and Ecuador, where it is a species of lowland and montane rain forest from sea level to 1700 m altitude.

Additional collections examined. COLOMBIA. **Antioquia:** Murri la Blanquita, Rio Murri (NW0676), Gentry *et al.* 75897 (K). **Valle:** Rio Anchicaya near CVC hydroelectric plant (NW0376), Gentry 35691 (K).

ECUADOR. **Carchi:** Tulcan Cantón, Awa Reserve (NW0178), *Quelal et al.* 625 (NY); Gualpi Alto (NW0078), *Thomson* 58856 (K); Cantón Tulcán, Tobar Donoso, Sector Sabalera (NW0178), *Tipaz et al.* 1296 (K); Lita (NW0078), *van der Werff et al.* 9571 (K, NY). **Esmeraldas:** San Lorenzo Canton, Awa Reserve, Centro Guadualito (NW0178), *C. Aulestia et al.* 305 (NY); Parroquia Mataje, Awa Reserve (NW0178), *C. Aulestia et al.* 583 (MO). **Imbabura:** valley of R. Mira (NW0078), *Pennington & Cruz* 10527 (K). **Pichincha:** Quito Cantón, Nanegal, Maquipucuna Reserva (NW0078), *Tipaz & Quelal* 181 (F, K).

- 45. *Guarea casimiriana*** Harms in Engler & Prantl., Nat. Pflanzenfam., ed. 2, 19b1: 133, 177 (1940); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 333, fig. 70 (1981). – Type: Peru, Loreto, Yurimaguas, fl., *Poeppig* 2261 (holo W; iso F, NY, OXF). **Fig. 55B.**

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 333 (1981).

Abbreviated description. Young shoots and inflorescences densely hispid with erect yellow stiff hairs, leaflets 32–39 × 9–10.5 cm, narrowly oblong or oblanceolate, chartaceous, with hispid indumentum on the lower surface, especially along the veins, venation brochidodromous, secondary veins 38–40 pairs, straight, parallel, inflorescence cauliflorous, a laxly-flowered spike to 13 cm long, petals c.16 mm long, densely golden strigose outside, staminal tube 12–13 mm long, 2–3 mm broad, anthers 9–10, ovary 6-locular, locules with 2 superposed ovules, fruit unknown.

Distribution and ecology. Known only from the type collection in Amazonian Peru, where it is a component of the understorey in lowland rain forest.

- 46. *Guarea constricta*** Al.Rodr., Lankesteriana 6: 106 (2006). – Type: Costa Rica, San José, Perez Zeledon, Savegre Abajo de Rio Nuevo, finca de Victor Julio Mena [NW0983], fl., *A. Estrada* 2016 (holo CR; iso INB, MO). **Figs 36, 60B.**

Young shoots stout, 1.2–1.5 cm diam., hollow, subglabrous, smooth, greyish brown, with sparse pale lenticels. *Leaves* pinnate with an inactive terminal bud, petiole 15–20 cm long, semiterete, glabrous, rhachis 27.5–33 cm long, terete or slightly channelled on the upper surface, glabrous; petiolule stout, 0.9–1.2 cm long. *Leaflets* opposite, 4 pairs, 30–50 × 10–18 cm, broadly elliptic, apex shortly acuminate, base acute to narrowly attenuate, glabrous, chartaceous, drying pale green; venation eucamptodromous, midrib not raised or sunken on the upper surface, secondaries 11–14 pairs, ascending, slightly arcuate and convergent, intersecondaries absent, tertiaries oblique. *Inflorescence* on branches below the leaves, 5–25 cm long, a panicle, the lowest lateral branches to 5 cm long, glabrous; pedicel 2–3 mm long (above the articulation). *Calyx* shallowly cup-shaped, 2–3 mm long, with shallow irregular obtuse lobes, glabrous. *Petals* 4, 12–14 × 2 mm, strap-shaped, apex acute, glabrous. *Staminal tube* 10–12 × 3 mm, flask-shaped, margin entire, glabrous; anthers 8, c.1 mm long, glabrous, dehiscent. *Nectary* a stout stipe expanded below the ovary, c.2 mm long, glabrous. *Ovary* c.3 mm long, ovoid, 4-locular, loculi with 2 superposed ovules, glabrous. *Capsule* 4.5–6 × 2.5–5 cm, broadly oblong, apex obtuse, not or scarcely constricted between the seeds, sometimes contracted at the base into a stout stipe c.1.8 cm long and 1 cm broad, 4-valved, valves with 2 superposed seeds, pericarp dark brown, rough or smooth, densely lenticellate, glabrous. *Seeds* c.3 × 1 cm; embryo with superposed cotyledons.

Field characters. Treelet or tree to 20 m high, inner bark pinkish. Flowers with white petals and yellow stamens, calyx green with red apices to the lobes. Flowering recorded in February, mature fruit in April.

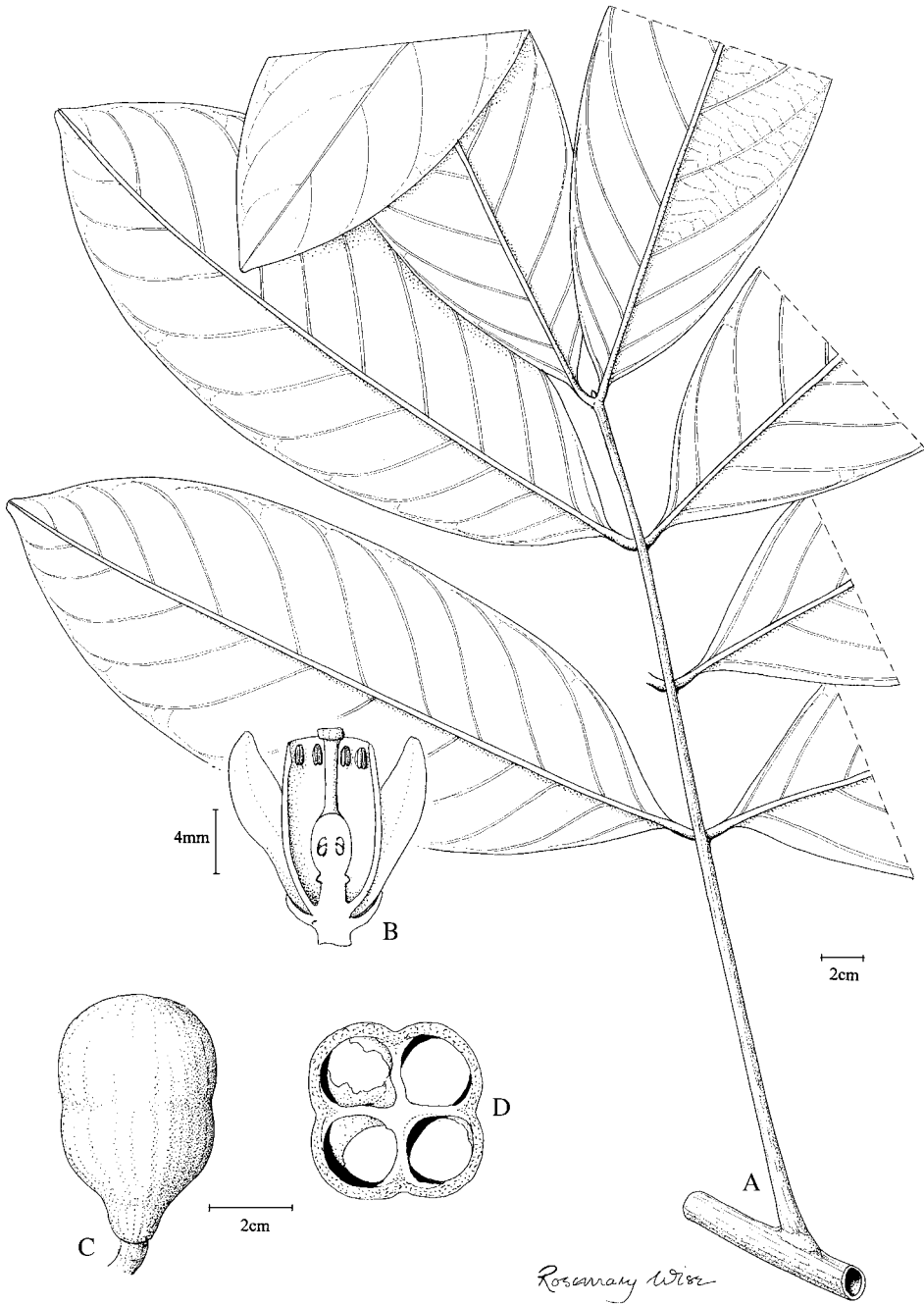


FIG. 36. *Guarea constricta* Al.Rodr. A, leaf; B, half-flower; C, fruit; D, cross-section of fruit. (A–D, Hammel & Robles 16760).

Distribution and ecology. In rain forest on the Pacific drainage of Costa Rica, from sea level to 1240 m altitude.

Collections examined. COSTA RICA. **Puntarenas:** Peninsula de Osa, Reserva Forestal Golfo Dulce, 10 km SW of La Palma (NW0883), *Hammel & Robles* 16760 (INB, MO); Golfito, R.N. Esquinas, Ridge Costeña/Cruces (NW0883), *Huber & Weissenhofer* 1566 (CR). **San José:** Cantón Perez Zeledon, Cuenca del Baru, Tinamaste (NW0983), *Rodríguez et al.* 139 (INB); Tarrazu, San Lorenzo, Quebrada Saletrillo (NW0984), *Rodríguez* 9617 (INB).

This species is similar to *Guarea bijuga*, differing only in the larger flowers with biovulate ovary locules and larger fruit. It may be distinguished by the hollow twigs, large leaflets which dry pale green, whole plant glabrous, petals 12–14 mm long, and large 4-valved fruit with 2 superposed seeds in each valve.

47. *Guarea convergens* T.D.Penn. in T.D.Penn. et al., *Fl. Neotrop.* 28: 260, fig. 53 (1981). – Type: Brazil, Amazonas, Manaus to Caracarai road, km 154, fl., *Pennington, Prance, Ramos & Monteiro* 9967 (holo INPA; iso FHO, MO, NY). **Fig. 49F.**

Abbreviated description. Indumentum inconspicuous, appressed puberulous or shortly pubescent, leaves with indeterminate apical growth, leaflets 3–12 pairs, 11.5–18.5 × 4–6 cm, elliptic oblong or oblanceolate, secondary veins 7–11 pairs, arcuate and convergent, inflorescence 5–17 cm long, a slender or pyramidal thyrses, petals 4, valvate, 6–7.5 mm long, staminal tube 5–5.5 mm long, 1.5–3 mm broad, anthers 7–8, ovary (3–)4-locular, locules 1-ovulate, capsule 2.5–4.5 cm long, 4-valved, ± globose, valves obscurely 6–7-ribbed and verruculose, minutely puberulous, pericarp 3–5 mm thick, without lenticels, valves 1-seeded.

Distribution and ecology. Southern Venezuela, French Guiana, central and western Brazilian Amazonia and Amazonian Peru, in lowland rain forest on non-flooded land.

Additional specimens examined. VENEZUELA. **Territorio Federal Amazonas:** San Carlos de Rio Negro, 20 km S of confluence of Rio Negro and Brazo Casiquiare (NW0167), *Clark & Maquirino* 7641 (K), 8354 (US).

FRENCH GUIANA. Bassin du Sinnamary, Crique Plomb (NW0553), *Loubry* 1774 (K).

PERU. **Loreto:** Centro de Investigaciones de Jenaro Herrera (SW0473), *Collector unknown*, Tree no.1-2/90 (K).

BRAZIL. **Acre:** Reserva INCRA Santa Luzia, km 40, BR-364 (SW0772), *Campbell et al.* 7077 (K). **Amazonas:** Reserva Florestal Ducke (SW0259), *Costa & Assunção* 384 (K), *Nascimento et al.* 590 (K), *Ribeiro et al.* 1698 (K).

48. *Guarea corrugata* Cuatrec., *Fieldiana, Bot.* 27: 72 (1950); T.D.Penn. in T.D.Penn. et al., *Fl. Neotrop.* 28: 343, fig. 75 (1981). – Type: Colombia, Dept. de Valle, Cordillera Occidental, Hoya del Rio Albán, fl., fr., *Cuatrecasas* 22337 (holo F; iso COL). **Fig. 55C.**

Abbreviated description. Young shoots and inflorescences minutely appressed puberulous, leaves with a terminal bud showing intermittent growth, leaflets up to

8 pairs, 18–25 × 5–11 cm, oblong-elliptic to elliptic, coriaceous, lower surface minutely sericeous at first, soon glabrous, secondary veins 12–16 pairs, inflorescence ramiflorous, up to 13 cm long, a slender panicle, petals 4, valvate, c.8 mm long (bud), sericeous outside, staminal tube c.6 mm long, c.3 mm broad, anthers 8–9, ovary 4-locular, locules with 2 superposed ovules, capsule c.5.5 cm long, c.3.5 cm broad, pyriform with c.16 longitudinal ridges each of which is conspicuously corrugate, minutely appressed puberulous, 4-valved, pericarp 6–7 mm thick, valves with 2 superposed seeds.

Distribution and ecology. Still known only from the type collection in western Colombia.

49. *Guarea corticosa* Al.Rodr., Lankesteriana 6: 107 (2006). – Type: Costa Rica, Puntarenas, Reserva Forestal Golfo Dulce, Rincón de Osa, Quebrada Banegas [NW0883], fr., *Aguilar* 488 (holo INB; iso MO). **Figs 37, 60C.**

Young shoots 8–10 mm diam., minutely appressed puberulous at first, soon glabrous, smooth, brown, becoming slightly suberous. *Leaves* pinnate with a terminal bud with intermittent growth, petiole 6–11.5 mm long, channelled above, glabrous, rhachis to 46 cm long, semiterete or terete, glabrous; petiolule swollen, 3–6 mm long. *Leaflets* opposite, up to 7 pairs, 26–38 × 13.5–19 cm, broadly elliptic, apex acuminate, base acute to obtuse or rounded, and often asymmetric on the lower leaflets, chartaceous, drying pale green, glabrous; venation eucamptodromous, midrib slightly sunken on the upper surface, secondaries 12–13 pairs, ascending, slightly arcuate, ± parallel, intersecondaries short or absent, tertiaries oblique. *Inflorescence* on larger twigs and trunk, a slender panicle c.2 cm long, flowers (not seen by me) subsessile. *Calyx* 3–4.5 mm long, with 3–4 shallow lobes, minutely appressed puberulous outside. *Petals* 4, 11–12.5 mm long, c.2 mm broad, apex acute, sericeous outside. *Staminal tube* 7–10.5 mm long, 3–3.5 mm broad, margin crenulate, glabrous; anthers 8, 1.75–2 mm long. *Nectary* a stipe 1–1.5 mm long. *Ovary* sericeous, 4–6(–8)-locular, locules with 2 superposed ovules, style 2.5–3 mm long, style-head discoid. *Capsule* 2–3 × 2.5 cm, globose to pyriform, truncate at apex and base, 6-valved, the valves irregularly ribbed and tuberculate, valves with 2 superposed seeds. *Seeds* c.1 cm long.

Field characters. Treelet to 6 m high with corky bark, flowers cream-coloured. Flowering recorded in May, fruiting in September and February.

Distribution and ecology. Known only from wet forest on the Pacific slopes of Costa Rica, up to 500 m altitude.

Collections examined. COSTA RICA. **Puntarenas:** Golfo Dulce, entrada a Chocuaco, Rincón (NW0883), *Aguilar* 312 (INB); PN Corcovado, Los Planes (NW0883), *Cordero* 253 (INB).

Species distinguished by the large leaflets with relatively few secondary veins and the small multivalved tuberculate/ribbed capsule.

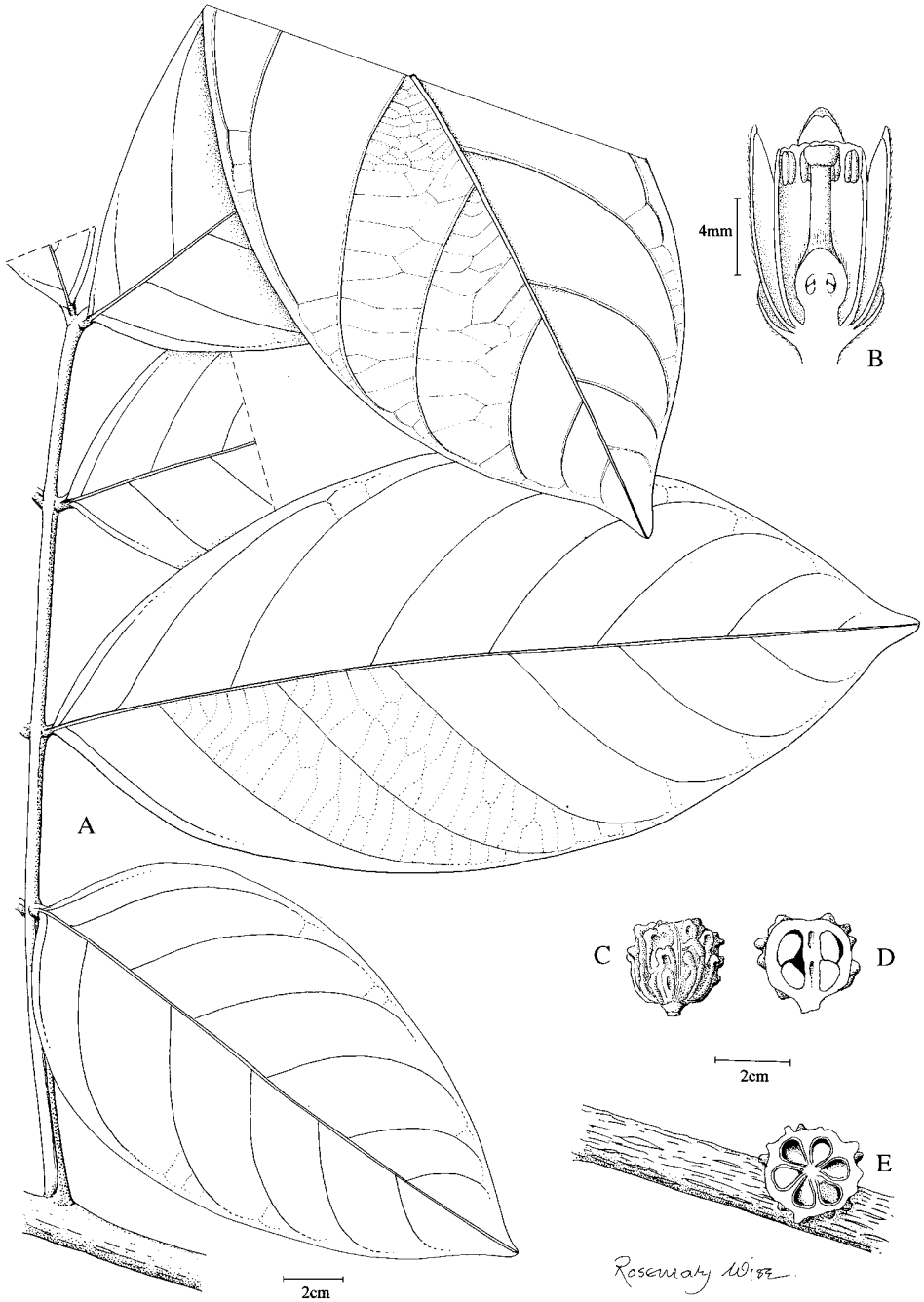


FIG. 37. *Guarea corticosa* Al.Rodr. A, leaf; B, half-flower; C, fruit; D, longitudinal section of fruit; E, cross-section of fruit. (A-C, E, Aguilar 488; D, Cordero 253).

- 50. *Guarea crispa*** T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 311, fig. 63 (1981).
– Type: Brazil, Amazonas, Manaus to Caracarai, km 28, fl., *Prance, Pena & Ramos* 3061 (holo INPA; iso F, FHO, GH, K, S). **Fig. 50A.**

Abbreviated description. Young shoots and inflorescences densely crisped-puberulous, twigs suberous and longitudinally fissured, leaves with a terminal bud showing intermittent growth, leaflets up to 5 pairs, 18–34 × 8–15 cm, broadly oblong or broadly elliptic, coriaceous, upper surface puberulous along the midrib, lower surface densely entangled- and crisped-puberulous, inflorescence axillary, 15–30 cm long, a pyramidal thyrse, petals 4–5, valvate, c.12.5 mm long, sericeous outside, staminal tube c.9 mm long, c.5 mm broad, anthers 8, ovary 4-locular, locules 1-ovulate, capsule 2.6–2.8 cm long, 2.7–3 cm broad, ± globose, apex truncate, base obtuse to rounded, smooth, densely puberulous, 4-valved, pericarp 2–3 mm thick, valves 1-seeded.

Distribution and ecology. Known only from central Brazilian Amazonia, where it is a component of non-flooded lowland forest.

Additional collections examined. BRAZIL. **Amazonas:** Dist. Agropecuario, Reserva 1501 (km 41) (SW0259), *Boom et al.* 8712 (K, NY); BR-174, km 72, Fazenda Dimona (SW0260), *da Silva* (INPA/WWF 2206.1225.2) (K); Fazenda Porto Alegre, Reserva 3304 (SW0259), *Pacheco et al.* 223 (K).

- 51. *Guarea donnell-smithii*** C.DC., Bull. Herb. Boissier, Sér. 2, 5: 419 (1905). – Type: Costa Rica, Boca Culebra, fl., *Pittier* 12093 (holo CR; iso G, NY (fragment), US; photo K). **Figs 38, 60D.**

Guarea glabra auct. non Vahl: T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 269 (1981), p.p.

Young shoots 2–4 mm diam., densely pilose-setose at first, becoming glabrous, smooth, pale whitish, without lenticels. *Leaves* pinnate with an active terminal bud, petiole 2–6 cm long, semiterete at first, becoming terete with age, pilose-setose at first, becoming glabrous, rhachis eventually up to 12 cm long, semiterete, pilose-setose at first, becoming glabrous; petiolule 2–3 mm long. *Leaflets* opposite, 1–4 pairs, 6–19 × 2.2–7.6 cm, elliptic or less frequently oblanceolate, apex narrowly acuminate to caudate, base acute, sometimes slightly asymmetric, chartaceous, upper surface glabrous except for pilose-setose midrib, lower surface sparsely pilose-setose on midrib and veins and with scattered hairs on the lamina, drying pale green, sometimes sparsely glandular-striate; venation eucamptodromous, midrib slightly sunken on the upper surface, secondaries (6–)10–12 pairs, ascending, slightly arcuate, slightly convergent, slightly sunken on the upper surface, intersecondaries absent, tertiaries few, oblique, parallel. *Inflorescence* axillary, 2–10 cm long, a few- and rather lax-flowered panicle with short lateral branches, sparsely setose-pilose; pedicel 1.5–2 mm long (above the articulation). *Flowers* unisexual (plant dioecious). *Calyx* 1–1.5 mm long, patelliform, with 4 shallow teeth or lobes, densely setose-pilose. *Petals* 4, 5–6 × 1–1.5 mm, strap-shaped, apex acute, free, valvate, pilose-setose outside, glabrous inside. *Staminal*

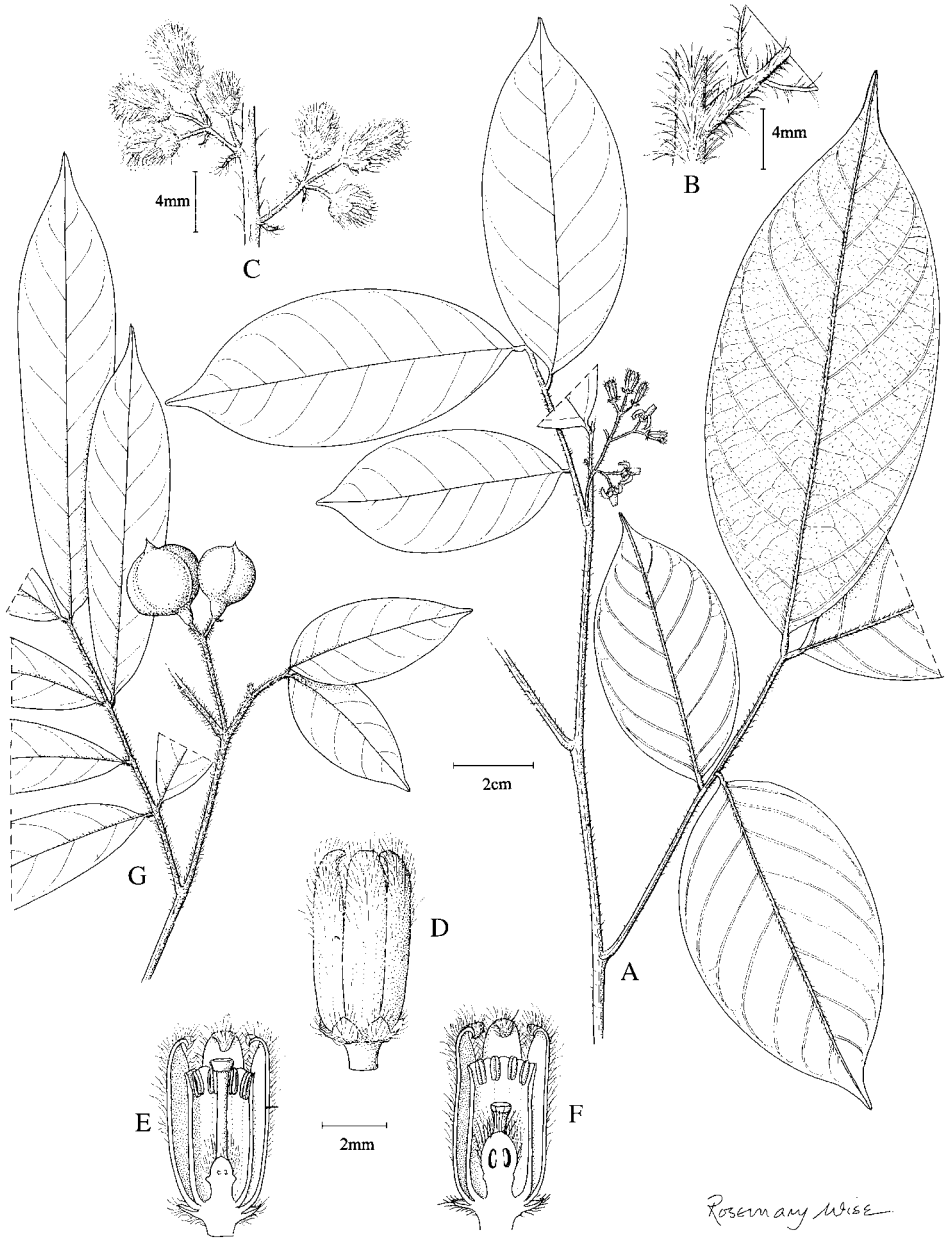


FIG. 38. *Guarea donnell-smithii* C.DC. A, habit; B, detail of indumentum; C, inflorescence; D, flower; E, half-flower (male); F, half-flower (female); G, fruit. (A, E, *Rodriguez et al.* 2140; B, G, *Brant & Hazlett* 2884; C, *Rodriguez* 7015; D, F, *Pittier* 13032).

tube 4-4.5 mm long, 4-angled in section, margin entire or slightly irregular, glabrous; anthers 8, c.1 mm long, oblong, glabrous, antherodes in female similar size but indehiscent and without pollen. *Nectary* in male a stipe c.1 mm long expanded into

a small collar below the ovary, glabrous, less evident in female. *Ovary* c.2 mm long, globose, 4-locular, locules 1-ovulate, sparsely pilose-setose, in male more slender and with rudimentary ovules, style c.2.5 mm long, glabrous, style-head discoid, about equalling the stamens. *Capsule* c.1.8 × 1.5 cm, globose, with a rounded apiculate apex and narrowed at the base to a short stipe 3–4 mm long, 4-valved, valves 1-seeded, pericarp c.1 mm thick, glabrous, smooth. *Seeds* 1–4, shaped like the segment of an orange; embryo not seen.

Field characters. Usually a small understorey treelet flowering when only a few metres high, but also recorded as a 25 m high tree. The flowers are pink or red and the mature fruit is red. Flowering occurs in January and February, with mature fruit in April and July. The mature fruit are sometimes accompanied by some flowering branches.

Distribution and ecology. Along the Atlantic drainage of Guatemala and Honduras and the Pacific drainage of Costa Rica, in lowland and lower montane rain forest from sea level to 1150 m altitude.

Collections examined. GUATEMALA. **Izabal:** 7 miles S of Puerto Barrios (NW1588), *Croat* 41809 (K).

HONDURAS. **Yoro:** Municipio Yoro, 0.9 km E of San José Texiguat, 3.5 km up R. Texiguat (NW1587), *Brant & Hazlett* 2884 (K).

COSTA RICA. **San José:** Cantón Pérez Zelendón, Cuenca del Barú, Tinamaste, Finca Tinamaste (NW0983), *Rodríguez et al.* 2140 (CR, MO), 2629 (CR); Cantón Perez Zelendón, Barú (NW0983), *Estrada et al.* 849 (CR); Cuenca del Savegre, Río Nuevo, El Brujo (NW0983), *Rodríguez et al.* 7015 (CR, MO).

This poorly known species occupies part of the range of *Guarea chiricana* (a member of the *Guarea glabra* complex) and is morphologically very close to it. Further collections may show them to be conspecific. They share many vegetative, floral and fruit characters, such as leaf shape, venation, texture, floral formula and fruit size. The only significant difference is the presence in *Guarea donnell-smithii* of coarse pilose-setose indumentum on the young shoots, calyx and outside of the petals. The petals and staminal tube of *Guarea donnell-smithii* are slightly shorter than those of *G. chiricana*. The Guatemala specimen cited above has much narrower leaflets than the type from Costa Rica, but the Honduran collection has both narrow leaflets and elliptical leaflets like those of the type.

52. *Guarea eriorhachis* Harms, Notizbl. Bot. Gart. Berlin-Dahlem 10: 244 (1928); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 357 (1981). – Type: Peru, Amazonas, mouth of R. Santiago [SW0477], fl., *Tessmann* 4450 (holo B, destroyed; iso F (fragment), MO (fragment)). **Figs 39, 55D.**

Leaves pinnate with a terminal bud showing intermittent growth, petiole c.13.5 cm long, semiterete above and slightly winged at the base, densely hirsute-villose (hairs 1–2 mm long), rhachis 50–60 cm long, semiterete, hirsute; petiolule 3–4 mm long,

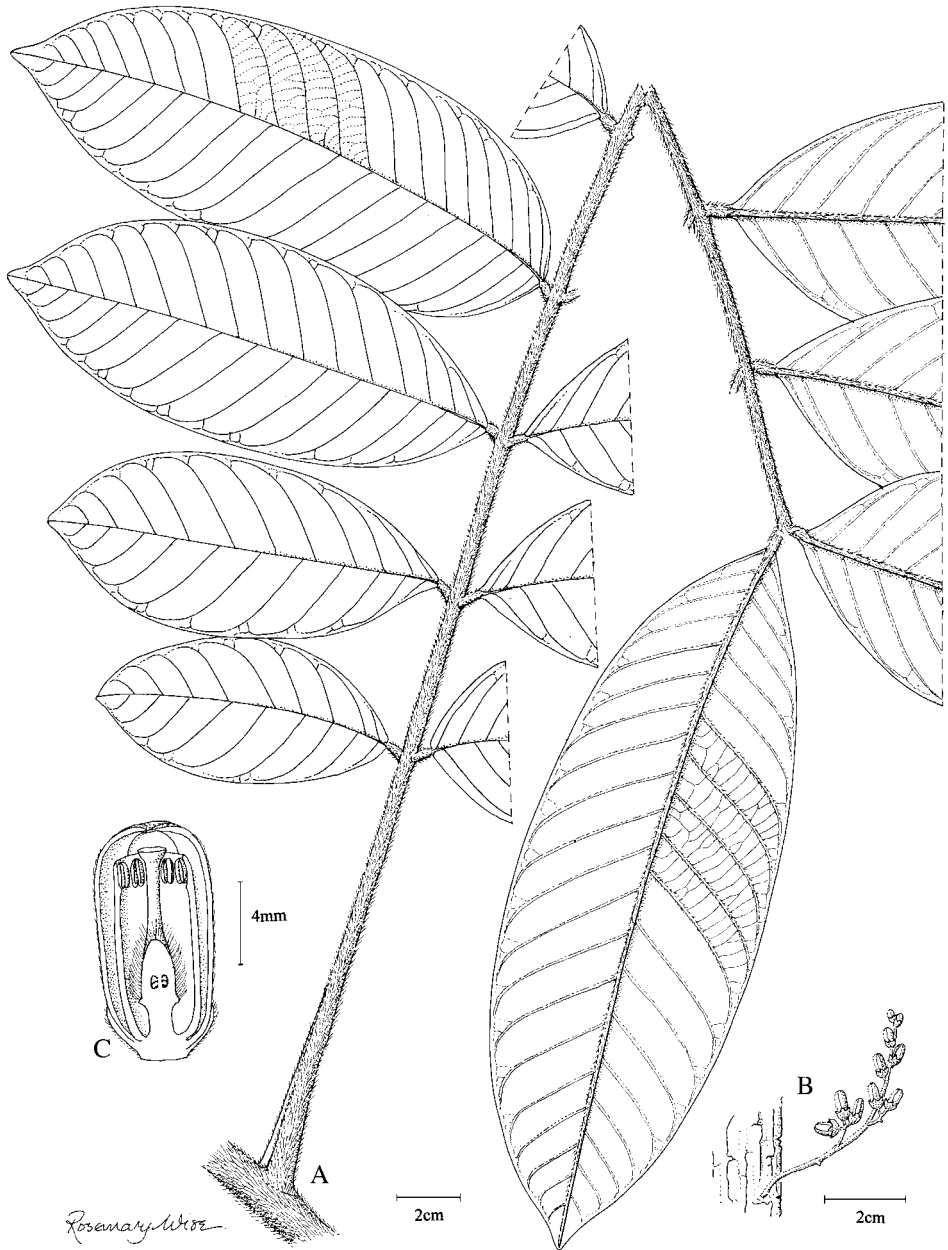


FIG. 39. *Guarea eriorhachis* Harms. A, habit; B, inflorescence; C, half-flower. (A–C, Schunke 5707).

densely hirsute-villose. *Leaflets* opposite, up to 8 pairs, 28–38 × 8.2–11 cm, oblanceolate, apex obtusely cuspidate, base acute, chartaceous, upper surface with pubescent midrib, otherwise glabrous, lower surface with densely hirsute-villose midrib and veins, sparser on the lamina, not glandular-punctate or -striate; venation eucamptodromous, midrib sunken on the upper surface, secondaries c.20 pairs, ascending, straight or slightly arcuate, parallel or slightly convergent, intersecondaries short or absent, tertiaries oblique, parallel. *Inflorescence* cauliflorous, 4–11 cm long, a slender panicle, with a few lateral branches to 2 cm long near the base, tomentose, ebracteate; pedicel c.1 mm long. *Calyx* cyathiform, 3–3.5 mm long, with 4 shallow, broadly ovate, obtuse lobes, pubescent outside, glabrous inside. *Petals* 4, valvate, free, 12–13 mm long, 2–3 mm broad, strap-shaped, apex acute, appressed pubescent outside, glabrous inside. *Staminal tube* 10–11 mm long, 3–3.5 mm broad, margin truncate, glabrous; anthers 8, c.1.5 mm long, glabrous. *Nectary* a stout stipe 1–1.5 mm long, expanded below the ovary, glabrous. *Ovary* c.3 mm long, ovoid, 4-locular, locules with 2 superposed ovules, densely covered in long stiff hairs, style 2–3 mm long, glabrous, style-head discoid. *Fruit* unknown.

Field characters. Treelet to 8 m high, with terminal clusters of large leaves, flowers with greenish yellow calyx and white petals. Flowering November to December.

Distribution and ecology. Known only from Amazonian Peru, where it is an understorey treelet of non-flooded lowland rain forest, up to 700 m altitude.

Collections examined. PERU. **San Martín:** Mariscal Caceres, Tocache Nuevo, Palo Blanco (SW0876), *Schunke* 5707 (F, K).

This species is morphologically similar to *Guarea casimiriana*, but differs in the far fewer secondary veins, smaller flowers and fewer ovary locules. The two species also have a different indumentum: that of *Guarea eriorhachis* is long, lax hirsute-villose, whereas that of *G. casimiriana* is hispid with stiff hairs. After studying more material of *Schunke* 5707, we are reasonably confident of placing it in this species. In its vegetative and floral morphology it is a close match to Harms' description.

53. *Guarea grossa* T.D.Penn., **sp. nov.** Figs 40, 61A.

A speciebus aliis capsula pergrandi, 5–6-valvata, valvae costis 3, crassis convexis grosse tuberculatis distinguenda. – Type: Costa Rica, Limón, Tortuguero National Park, Tortuguero-Sierpe basin, Lomas de Sierpe, 1.5 km W of National Park Post on R. Sierpe [NW1083], fr., viii 1988, *Robles, Herrera & Flores* 2016 (holo K; iso INB).

Young shoots 6–7 mm diam., finely appressed puberulous, smooth, brown. *Leaves* pinnate, terminal bud ?fallen, petiole 6–9 cm long, narrowly winged at the base, finely appressed puberulous, rhachis 20–25 cm long, terete, subglabrous; petiolule 7–10 mm long. *Leaflets* opposite, 5–6 pairs, the largest (terminal) c.18–19 × 6–7 cm, elliptic to oblong, apex acuminate, base narrowly attenuate or acute, chartaceous,

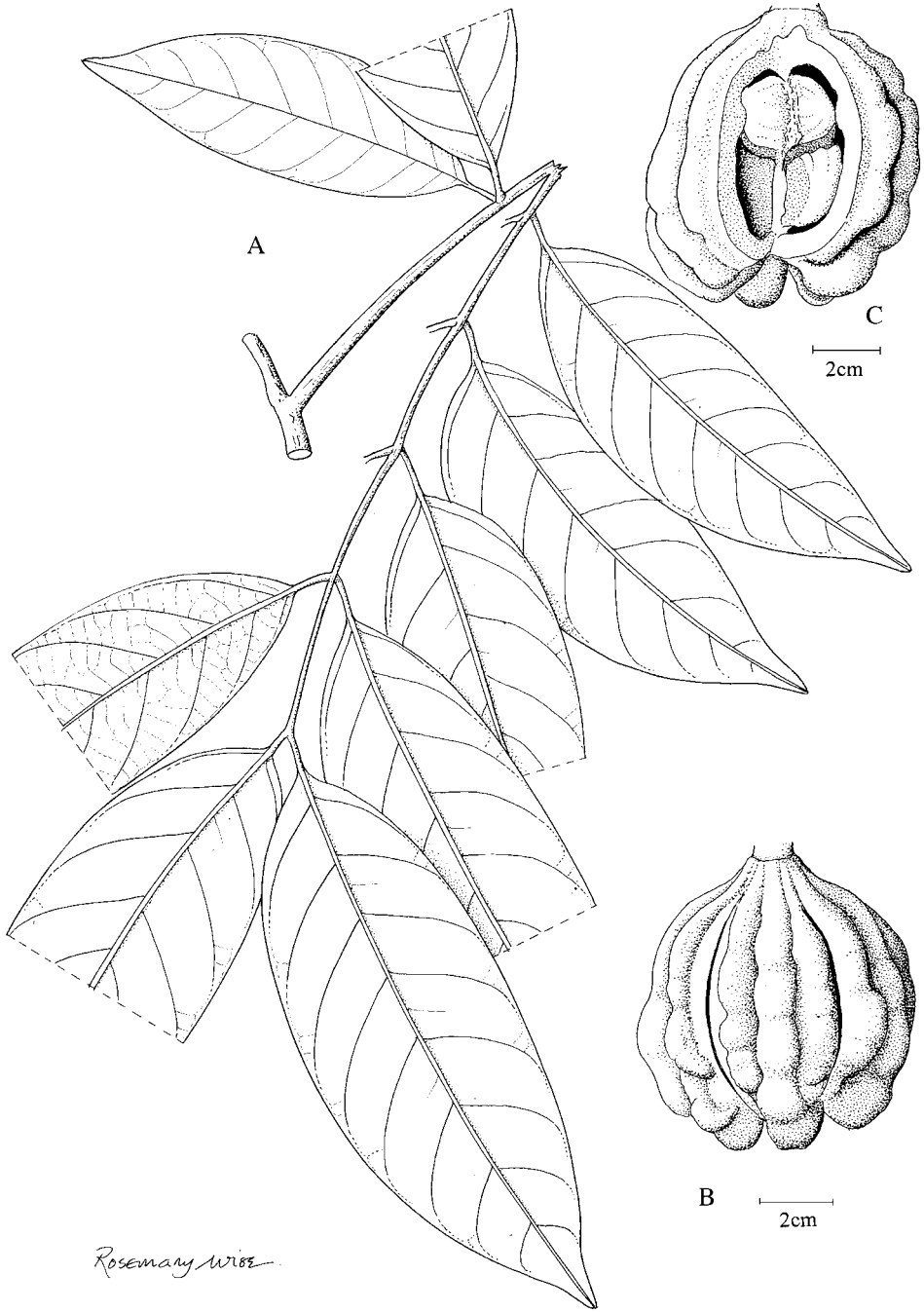


FIG. 40. *Guarea grossa* T.D.Penn. A, leaf; B, fruit; C, longitudinal section of fruit. (A–C, Robles et al. 2016).

glabrous, not glandular-punctate or -striate; venation eucamptodromous, midrib flat on the upper surface, secondaries 9–10 pairs, ascending, slightly arcuate and convergent, intersecondaries short to moderately long, tertiaries oblique, obscure. *Flowers* unknown. *Capsule* ?solitary, 9.5–10.5 × 9–9.5 cm, broadly pyriform, apex depressed, tapering at the base to a short thick annulus c.2.5 cm broad, 5–6-valved, pericarp woody when dry, 0.8–1.2 cm thick, each valve with 3 longitudinal convex ribs, the central one longer than the 2 lateral ones and coarsely branched and tuberculate towards the apex, ribs 0.8–1.5 cm broad, glabrous, valves with 2 superposed seeds. *Seeds* c.3 × 2 × 2 cm, truncate at apex or base, completely surrounded by a thick fleshy sarcotesta. *Seed coat* thin, cotyledons free, superposed, radicle abaxial and slightly exerted.

Field characters. Unbuttressed tree to 25 m high, with smooth bark. According to the field data, the fresh fruit measure 15 × 15 cm. There is no information on fruit colour, dehiscence or dispersal. Fruiting occurs in August.

Distribution and ecology. Known only from a single collection on the Caribbean drainage of Costa Rica. It was collected in lowland rain forest on well-drained slopes, around 100 m altitude.

The general form and venation of the leaves of this species is similar to that of the widespread *Guarea grandifolia*, which also has a multilocular fruit with 2 superposed seeds in each valve. However, the capsule of *Guarea grossa* is much larger and very distinct in the prominent rounded and tuberculate ribs.

54. *Guarea hoffmanniana* C.DC. in A.DC. & C.DC., Monogr. Phan. 1: 570 (1878); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 357 (1981). – Type: Costa Rica, Heredia, Pedregal, *Wendland* [*Hoffmann*] 755, fl. (holo B, destroyed; lecto GOET n.v. (photos seen), designated by Grayum (2006: 1007); isolecto F, GH, MO n.v.). See Grayum (2006: 1007) for commentary. **Fig. 55E.**

Guarea macropetala T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 349, fig. 74 (1981). – Type: Panama, Province Panamá, El Llano to Carti road, fl., *Nee & Tyson* 10989 (holo MO; iso K, NY).

Abbreviated description. Young shoots golden-tomentose or villose, inflorescence golden puberulous, leaves with a terminal bud showing intermittent growth, leaflets up to 5 pairs, 14.5–23 × 5–9 cm, broadly oblong or oblanceolate, sparsely to densely pubescent on midrib and veins, lamina generally glabrous, upper surface bearing numerous minute raised dots, secondaries 11–14 pairs, inflorescence cauliflorous, solitary or paired, a raceme or slender panicle, with a few short lateral branches at the base, petals 4, valvate, 15–18 mm long, golden sericeous outside, staminal tube 10–13 mm long, anthers 10–13, 2–2.2 mm long, ovary 7–10-locular, locules with 2 superposed ovules, capsule c.5.5 × 6 cm, broadly pyriform, strongly depressed at the apex, tapering at the base, contracted between the valves when dry and somewhat

tuberculate, puberulous, 7–10-valved, valves with 2 superposed seeds, pericarp 5–7 mm thick.

Distribution and ecology. Costa Rica and Panama, in lowland and lower montane rain forest up to 700 m altitude.

Additional collections examined. COSTA RICA. **Heredia:** Cantón Sarapiquí, La Virgen (NW1083), *Zamora et al.* 2535 (INB); Rio Puerto Viejo, Finca la Selva (NW1084), *Folsom* 9843 (F), *Grayum* 1146 (F). **Limón:** Guápiles, Finca las Laureles de Corinto (NW1083), *Pennington & Zamora* 13343 (CR, K).

PANAMA. **Bocas del Toro:** Fortuna Dam region (NW0882), *McPherson* 8413 (K); road towards Chiriquí Grande (NW0882), *McPherson* 12547 (K). **Cocle:** between Caño Blanco del Norte, Caño Suncio and Chorro del Rio Tife (NW0880), *Davidse & Hamilton* 23533 (K, MEXU). **Colón:** Santa Rita Ridge (NW0979), *McPherson* 10244 (K). **San Blas:** El Llano–Carti road km 19.1 (NW0978), *de Nevers et al.* 5202 (K), 5366 (K), 5869 (K).

55. *Guarea humaitensis* T.D.Penn. in T.D.Penn. et al., *Fl. Neotrop.* 28: 306, fig. 62 (1981). – Type: Brazil, Amazonas, Manaus to Porto Velho road, km 345, fl., *Pennington, Prance, Ramos & Monteiro* 9995 (holo INPA; iso FHO, NY). **Fig. 50B.**

Abbreviated description. Young shoots and inflorescences puberulous to pubescent, leaves with a dormant terminal bud without intermittent growth, leaflets 5–7 pairs, (14–)20–27.5(–31) × 5.9–8.8(–9.5) cm, usually oblanceolate, rarely elliptic or oblong, thinly coriaceous, with some pubescence along the lower midrib, otherwise glabrous, secondary veins 11–16 pairs, inflorescence axillary or on twigs below the leaves, 10–30(–40) cm long, a laxly-branched panicle, lower lateral branches to 10 cm long, petals 4–5, valvate, 9–13 mm long, staminal tube (7–)8–11 mm long, (2–)3–6 mm broad, anthers 8–9, ovary 4–5-locular, locules 1-ovulate, capsule 1.8–3 cm long, globose to ovoid, apiculate, base contracted into a short stipe c.0.5 cm long, 4–5-valved, each valve with 3–5 longitudinal wrinkled ribs, puberulous, pericarp c.2 mm thick, valves 1-seeded.

Distribution and ecology. Central to western Amazonian Brazil, in non-flooded lowland rain forest. A single recent collection from French Guiana (*Prévost & Grenand* 4329) may belong to this species, but without flowers or fruit it cannot be placed with certainty.

Additional collections examined. BRAZIL. **Amazonas:** Manaus, Reserva Florestal Ducke (SW0259), *Assunção & Vicentini* 1 (K), *Assunção et al.* 809 (K); Município de Novo Aripuaná BR 230, 400 km from Humaita (SW0760), *Cid Ferreira* 5920 (K); Dist. Agropecuario, Reserva 1501, km 41 (SW0259), *Freitas et al.* 536 (K); km 26 Manaus – Itacoatiara road, Ducke Reserve (SW0259), *Gentry et al.* 69064 (K), *Gentry & Nelson* 69276 (K); Município Manaus, 90 km N of Manaus, Fazenda Dimona (SW0260), *Kukle* 72 (K, NY); Dist. Agropecuario, Reserva 1501 WWF/INPA project (SW0259), *Oliveira et al.* 164 (K), *Pacheco et al.* 118 (K); Manaus, Ducke Reserve (SW0259), *Sothers* 213 (K), *Sothers & Silva* 659 (K).

56. *Guarea inesiana* Al.Rodr., Lankesteriana 6: 109 (2006). – Type: Costa Rica, San José, Desamparados, Cuenca del Reventazon, Cerros de la Muerte [NW0983], fr., *A. Rodríguez* 9624 (holo INB). **Fig. 61B.**

Young shoots 7–8 mm diam., finely puberulous, becoming glabrous, pale brown, lenticellate. *Leaves* pinnate with intermittent apical growth, petiole 5–6 cm long, semiterete, glabrous, rhachis up to 20 cm long, semiterete, glabrous; petiolule 1.2–1.5 cm long, swollen. *Leaflets* opposite, up to 5 pairs, 17–26 × 6–9 cm, broadly oblong to oblanceolate, apex obtuse to shortly cuspidate, base acute to narrowly cuneate, coriaceous, glabrous except for tufts of hair in the axils of the secondary veins below; venation eucamptodromous, midrib not raised or sunken on the upper surface, secondaries 10–11 pairs, steeply ascending, mostly ± straight, parallel to slightly convergent, intersecondaries short or absent, tertiaries oblique, numerous. *Inflorescence* on twigs below the leaves, 5–8 cm long, a pyramidal panicle, subglabrous; pedicel 1–2 mm long (above the articulation). *Calyx* shallowly cup-shaped, 2–3 mm long, irregularly toothed or lobed, subglabrous. *Petals* 4, 11–12 mm long, strap-shaped, apex acute, glabrous apart from sparse minute appressed hairs near the apex. *Staminal tube* 10–11 mm long, 4–5 mm broad, margin truncate, glabrous; anthers 8–9, c.1.5 mm long, glabrous. *Nectary* c.1.5 mm long, glabrous. *Ovary* 4-locular, locules with 2 superposed ovules, subglabrous, style-head discoid. *Capsule* 7–7.5 cm diam., globose, apex and base rounded, 4-valved, valves smooth, densely lenticellate, glabrous, pericarp (when dry) 1.3–1.5 cm thick, valves with 2 superposed seeds. *Seeds* c.2 cm long, plano-convex; embryo with plano-convex, superposed cotyledons, radicle abaxial, extending to the surface.

Field characters. Tree to 30 m high with scaling bark and pink slash, leaves up to 50 cm long. Flowers cream, anthers brown and fruit maturing red. Flowering recorded in March, mature fruit in June.

Distribution and ecology. Costa Rica, on the Pacific slopes of the Cordillera Central and on the Cordillera de Talamanca, in montane rain forest between 1740 m and 2000 m altitude.

Collections examined. COSTA RICA. **Alajuela:** Reserva Forestal Grecia, Bosque Eterno de los Niños, Sendero Pinares (NW1084), *L.D. Vargas* 1233 (INB).

Morphologically close to *Guarea kunthiana*, and differing from it only in the presence of hair tufts in the vein axils on the lower leaflet surface. Similar large-fruited forms of *Guarea kunthiana* are known from high altitude forest in the Andean countries.

57. *Guarea juglandiformis* T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 301, fig. 61 (1981). – Type: Brazil, Acre, road Cruzeiro do Sul to Japiim, km 18, fl., *Prance, Pena & Ramos* 2837 (holo INPA; iso FHO, NY, S). **Fig. 50C.**

Abbreviated description. Young shoots closely appressed puberulous and papillose, leaves with indeterminate apical growth, leaflets 2–7 pairs, 16–22 × 5–7 cm, oblong,

elliptic or lanceolate, base narrowly attenuate, chartaceous, lower surface puberulous, secondary veins 10–12 pairs, tertiary venation easily visible, inflorescence up to 35 cm long, a slender thyrse, petals 4, valvate, c.5.5 mm long, staminal tube c.4 mm long, c.1.25 mm broad, anthers 8, ovary 4-locular, locules 1-ovulate, capsule 2.5–3 cm long, globose to broadly pyriform, 4-valved, each valve with 3 slender, convoluted and anastomosing wings, up to 7 mm deep, sparsely puberulous, pericarp (excluding wings) 2–5 mm thick, valves 1-seeded.

Distribution and ecology. Western Amazonian Brazil and Amazonian Peru, in non-flooded lowland forest on lateritic soils, below 400 m altitude.

Additional collections examined. PERU. **Loreto:** Maynas, Nauta-Iquitos (SW0473), Ayala 1690 (NY); Iquitos-Nauta km 28 (SW0373), Rimachi 11842 (NY), 12160 (NY); Iquitos-Nauta km 48 (SW0473), Vásquez 7122 (NY); Allpahuayo, IIAP Station (SW0373), Vásquez *et al.* 13825 (MO, QCNE), van der Werff *et al.* 10247 (MO).

BRAZIL. **Amazonas:** Município de Novo Aripuaná, BR230, 300 km from Humaitá (SW0760), Cid Ferreira 5712 (K); 400 km from Humaitá (SW0760), Cid Ferreira 5973 (K). **Rondonia:** Município Costa Marqués, BR-429, INCRA project Porto Murinho (SW1263), Cid Ferreira 8646 (K).

58. *Guarea lozanii* M.E.Morales, Rev. Acad. Colomb. Cienc. 22(84): 336 (1998).

– Type: Colombia, Vaupés, Município de Taraira, Caparú Biological Station, 3 km N of Lake Taraira [SW0169], fl., Defler 295 (holo COAH; iso COAH, MO).

Fig. 56A.

Young shoots pubescent at first, soon glabrous, c.1 cm diam., smooth, brown. *Leaves* pinnate with a terminal bud, petiole 17–20 cm long, channelled on the upper surface, subglabrous, rhachis 35–40 cm long, terete, glabrous; petiolule 4–5 mm long, swollen. *Leaflets* opposite, 6–7 pairs, 28–33 × 7–9.4 cm, oblanceolate, apex narrowly acuminate, base acute to narrowly cuneate, chartaceous, upper surface with pubescent midrib, lower surface glabrous, not glandular-punctate or -striate; venation eucamp-todromous, midrib sunken on the upper surface, secondaries 23–24 pairs, ascending, slightly arcuate, slightly convergent, intersecondaries absent, tertiaries oblique, obscure. *Inflorescence* ramiflorous, 5–18 cm long, a slender panicle with some lateral branches near the base to 1 cm long, flowers subtended by small ovate bracts c.1 mm long; pedicel 4–10 mm long. *Calyx* cup-shaped, 4–5 mm long, 4–5-lobed to about 1/2 its length, sparsely puberulous. *Petals* 4–6, valvate, c.10 × 2 mm, strap-shaped, apex acute, finely appressed puberulous outside, glabrous inside. *Staminal tube* c.7 × 2 mm, margin entire, glabrous; anthers 9–11, c.1.5 mm long, oblong, with a short terminal appendage, dehiscent, glabrous. *Nectary* c.2 mm long, a stout stipe expanded below the ovary, glabrous. *Ovary* narrowly ovoid, 6-locular, locules with 1 ovule, sparsely pubescent, style sparsely pubescent below, glabrous above, slightly shorter than the staminal tube, style-head discoid. *Fruit* unknown.

Field characters. Tree to 15 m high and 16 cm diam., flowering in August.

Distribution and ecology. Described from lowland rain forest in Amazonian Colombia, with a second possible record from lowland Amazonian Peru.

Collections examined. PERU. **Ucayali:** Pucallpa-Tingo Maria km 84, von Humboldt Reserve (SW0875), *Pennington et al.* 17066 (K, MOL).

Without fruit, the relationships of this species remain doubtful. In general leaf and floral morphology it is similar to both *Guarea venenata* and *G. purusana*, but both these species generally have biovulate ovary locules and somewhat larger flowers. *Guarea lozanii* has anthers terminated by a short appendage, and this is also occasionally seen in *G. purusana*. The ovary of *Guarea lozanii* is slightly longitudinally ribbed, which may indicate that it has a winged or ribbed fruit. If so, then this would place the species in the vicinity of *Guarea caulobotrys* or *G. fistulosa*.

59. *Guarea megacostata* T.D.Penn., sp. nov. Figs 41, 66C.

Guarea grandifoliae affinis sed ovario 4-loculare, loculis uniovulatis, capsula 4-valvata, manifeste 12-costata differt. – Type: Venezuela, Carabobo, above headwaters of R. San Gian, E of Los Tanques, S of Borburata [NW1067], fr., iii 1966, J.A. & C. Steyermark 95392 (holo K; iso US).

Young shoots massive, 1.5–2.5 cm diam., densely and coarsely tomentose with pale hairs, becoming glabrous, without lenticels. *Leaves* pinnate with an active terminal bud, petiole 15–20 cm long, deeply channelled above at base to slightly channelled at apex, rhachis 15–25 cm long, slightly channelled above, petiole and rhachis pubescent at first, becoming glabrous; petiolules swollen, c.5 mm long. *Leaflets* opposite, 1–3 pairs, first pair 17–17.5 × 12.5–13.5 cm, suborbicular, apex truncate, base rounded, subsequent pairs 25–30 × 11.5–13.5 cm, broadly oblong-elliptic, apex rounded, base acute to obtuse, coriaceous, upper surface glabrous, lower surface with sparsely pubescent midrib, not glandular-punctate or -striate; venation eucamptodromous, midrib flat or slightly sunken, secondaries 10–12 pairs, ascending, straight or slightly arcuate, parallel, intersecondaries absent, tertiaries numerous, oblique; higher order reticulum obscure. *Inflorescence* borne below the leaves. *Flowers* not seen. *Capsule* pendulous on a peduncle at least 7 cm long (incomplete), c.5 × 4 cm (according to field data the mature fruit is 7–8 cm long and 6–7 cm broad), obovoid, apex obtuse, tapering to an acute base, 4-valved, pericarp woody, 7–8 mm thick, each valve bearing 3–4 thick prominent longitudinal ribs, 3–4 mm high, finely appressed puberulous; valves 1-seeded. *Seed* c.2.3 × 1 cm, ellipsoid, apex rounded, base acute, completely surrounded by a thin fleshy sarcotesta. *Seed coat* thin, cotyledons superposed, radicle abaxial, extending to the surface.

Field characters. Tree to 15 m high with pendent fruit on elongated peduncles. The fruit matures wine-red. Fruiting in March.

Distribution and ecology. Known only from evergreen lower montane forest in Carabobo and Falcón, Venezuela, at an altitude between 750 m and 1100 m.

Collections examined. VENEZUELA. **Falcón:** road Riecita – La Mina (NW1068), *Cardozo* 147 (K).

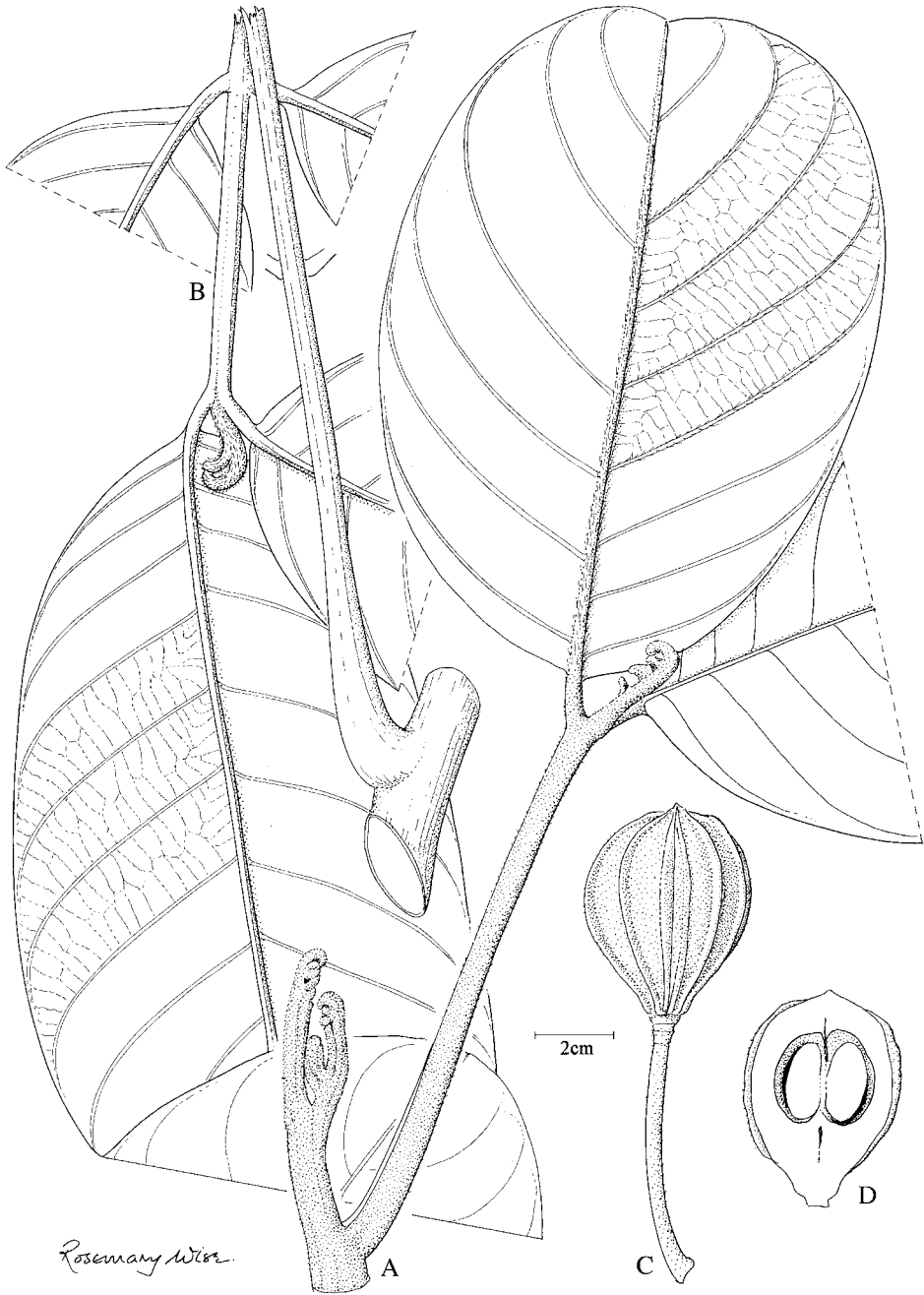


FIG. 41. *Guarea megacostata* T.D.Penn. A, B, habit; C, fruit; D, longitudinal section of fruit. (A–D, Steyermark, J. A. & C. 95392).

The large size and form of the leaves of this species are similar to those of the widespread *Guarea grandifolia*, but it differs from that species in its uniformly 4-locular ovary with uniovulate loculi (ovary (4-)7-8(-10)-locular, loculi with 2 superposed ovules in *G. grandifolia*), and in the strongly ribbed capsule (smooth or only faintly lined in *G. grandifolia*).

Guarea carinata has a somewhat similar fruit but it differs in its more numerous ovary loculi, each with 2 superposed ovules, and in its smaller leaflets and distinctive indumentum.

60. *Guarea mexicana* Coronado, Novon 16: 465 (2006). – Type: Mexico, Chiapas, Bochil, road from Bochil to Simojovel, 4.5 miles NE of Bochil, *Breedlove* 10220 (holo NY). **Figs 42, 61C.**

Young shoots 4–5 mm diam., shortly pubescent at first, becoming glabrous, often longitudinally striate (when dry), becoming smooth, pale greyish-buff, with a few large lenticels. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 3.5–6 cm long, semiterete, shortly pubescent, rachis up to 12 cm long, semiterete, shortly pubescent; petiolule 4–5 mm long, shortly pubescent. *Leaflets* opposite, up to 4 pairs, 14.2–22.5 × 3.9–5.2 cm, oblong to oblong-elliptic, apex shortly acuminate, base acute to obtuse and sometimes slightly asymmetric, margin slightly recurved near the base, coriaceous, upper surface glabrous, lower surface shortly pubescent along the midrib and secondary veins, not glandular-punctate or -striate; venation eucamptodromous, midrib sunken on the upper surface, secondary veins 8–10 pairs, ascending, arcuate, slightly convergent, intersecondaries short or absent, tertiaries oblique to perpendicular, venation rather conspicuous on both surfaces (when dry). *Inflorescence* axillary, 3–6 cm long, a slender panicle with short lateral branches to 1.5 cm long, shortly pubescent; pedicel c.1 mm long. *Flowers* unisexual (plant dioecious) (male flowers only seen). *Calyx* 3–3.5 mm long, cup-shaped, 4-lobed for 1/3 to 1/2 its length, lobes ovate, obtuse or rounded, subglabrous. *Petals* 4, c.8 × 2 mm, strap-shaped, apex acute, finely appressed puberulous outside, glabrous inside. *Staminal tube* broadly cylindrical, 6–6.5 × 3 mm, margin undulate, glabrous; anthers 8, c.1 mm long, oblong, glabrous. *Nectary* a stout stipe 1–1.5 mm long, slightly expanded below the ovary, glabrous. *Ovary* ovoid, c.1.5 mm long, 4-locular, locules uniovulate (rudimentary in male), glabrous, style 2.5–3 mm long, style-head discoid. *Capsule* c.2.5 cm diam., globose, apex rounded or truncate, base rounded, 4-valved, valves 1-seeded, pericarp rough and densely lenticellate, glabrous. *Seeds* not seen.

Field characters. Tree to 18 m high, flowering in May, with mature fruit in December.

Distribution and ecology. Southeastern Mexico (Chiapas) where it occurs in lower montane rain forest over limestone, associated with *Quercus*, *Billia*, *Persea*, *Nectandra*, *Aphananthe*, *Turpinia* and *Calatola*, altitudinal range 900–1000 m. According to

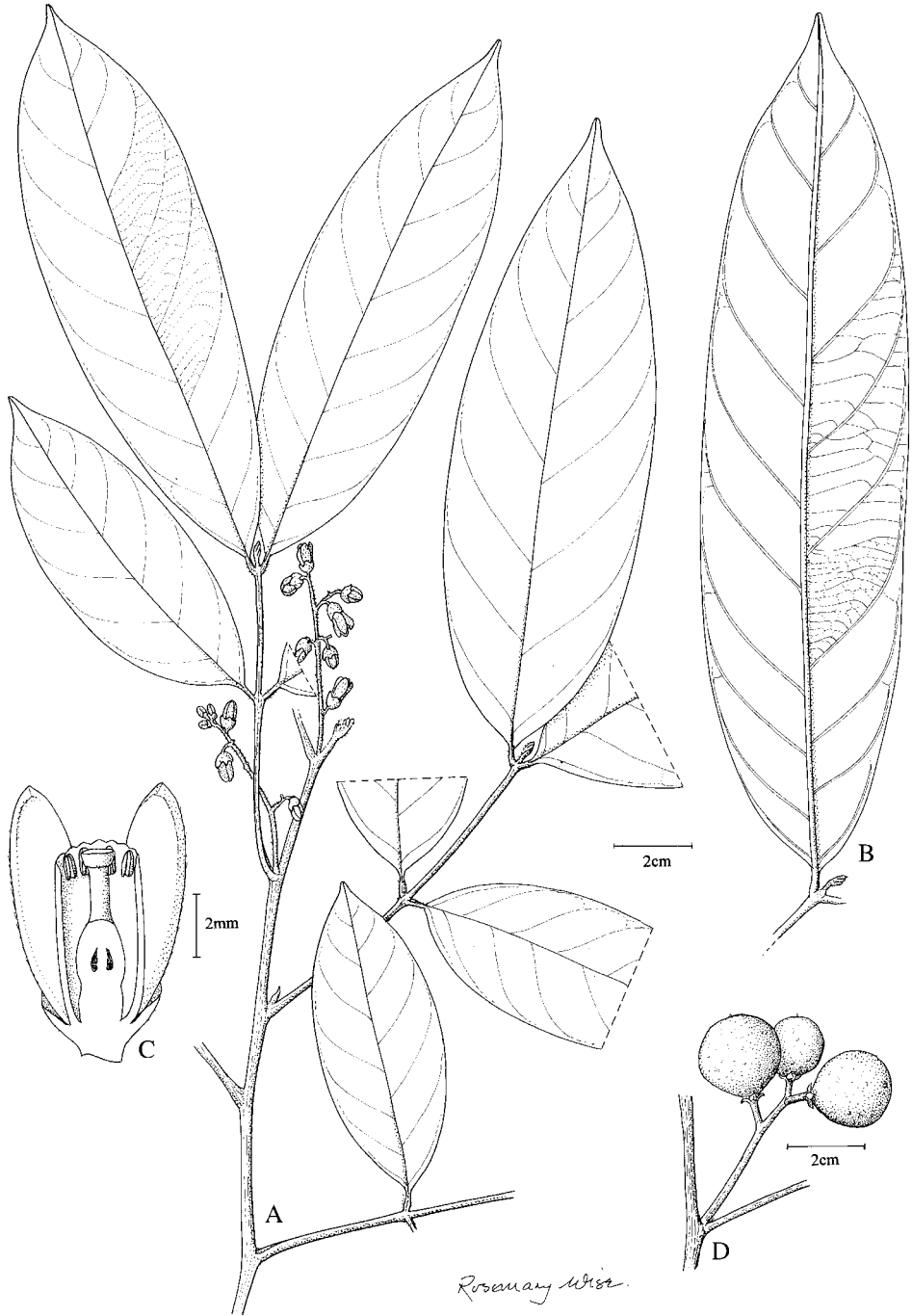


FIG. 42. *Guarea mexicana* Coronado. A, habit; B, leaflet; C, half-flower; D, fruit. (A, D, Breedlove & Thorne 30774; B, Breedlove 20245; C, Breedlove 35320).

Coronado it also occurs in Honduras (*Williams & Molina* 14655), but we have not seen this specimen.

Collections examined. MEXICO. **Chiapas:** 13 km N of Berriozabal, near Pozo Turipache and Finca El Suspiro (NW1693), *Breedlove* 20245 (F, MO), 35320 (MO, NY), *Breedlove & Smith* 21678 (MO), *Breedlove & Thorne* 30774 (MO).

This species probably belongs in the *Guarea glabra* complex. Its leaf morphology is similar to that of *Guarea glabra* subsp. *glabrescens*, except that it has fewer secondary veins and it also differs in its larger flowers with a glabrous ovary. The floral morphology is closest to *Guarea bijuga*, but it differs from this in its pubescent petals. The leaflets of *Guarea mexicana* are more slender than those of *G. bijuga*, and pubescent along the lower midrib and secondary veins.

61. *Guarea polymera* Little, J. Wash. Acad. Sci. 38: 98 (1948); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 318, fig. 65 (1981). – Type: Ecuador, Esmeraldas, S of Playa de Oro, fl., *Little* 6404 (holo US; iso F, K, NY, U, Y). **Fig. 56B.**

For synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 318 (1981).

Abbreviated description. Young shoots and inflorescences minutely papillose, leaves with a dormant non-active terminal bud, leaflets (3–)4–7 pairs, 20–30 × 5–8.8 cm, oblong to oblanceolate, thinly coriaceous, glabrous above, minutely appressed puberulous below, venation eucamptodromous, inflorescence axillary, 10–36 cm long, a broad, laxly-branched and laxly-flowered panicle, lowest lateral branches to 12 cm long, petals 5–7, valvate, 10–15 mm long, staminal tube, contracted at the throat, c.8 mm long, 5–7 mm broad, anthers 10–11, ovary 6–7-locular, locules with 2 superposed ovules, minutely appressed puberulous, capsule 3–4 cm diam., globose, smooth, densely papillose, 6–7-valved, pericarp 3–4 mm thick, valves with 2 superposed seeds.

Distribution and ecology. Pacific drainage of Colombia and Ecuador where it is confined to lowland rain forest, up to 500 m altitude.

Additional collections examined. COLOMBIA. **Chocó:** Municipio de Pizarro, Rio Pepe (NW0577), *Espina* 2059 (MO); Baudo (NW0477), *Fuchs & Zanella* 22356 (US). **Nariño:** Tumaco-Tuquerres, E of Llorente (NW0178), *Gentry* 34931 (COL).

ECUADOR. **Esmeraldas:** San Lorenzo, Awa Reserva (NW0178), *C. Aulestia* 942 (MO, NY); El Siléncio (NW0079), *Cornejo & Bonifaz* 6603 (K); San Miguel, Rio Cayapas, Loma Linda (NW0078), *Tipaz et al.* 2276 (MO); San Miguel, Limones, Rio Grande (NW0078), *Tipaz et al.* 2283 (K); Eloy Alfaro, Cotocachi Cayapas Reserve, San Miguel (NW0078), *Tipaz* 2480 (NY, QCNE), 2652 (QCNE).

62. *Guarea reticulatovenosa* T.D.Penn., sp. nov. **Figs 43, 56C.**

Guarea sprucei affinis sed foliolorum nervibus secundariis 23–26-jugis, inflorescentia cauliflora, ovario 4-loculare, fructu stipitato leviter costato differt. – Type:

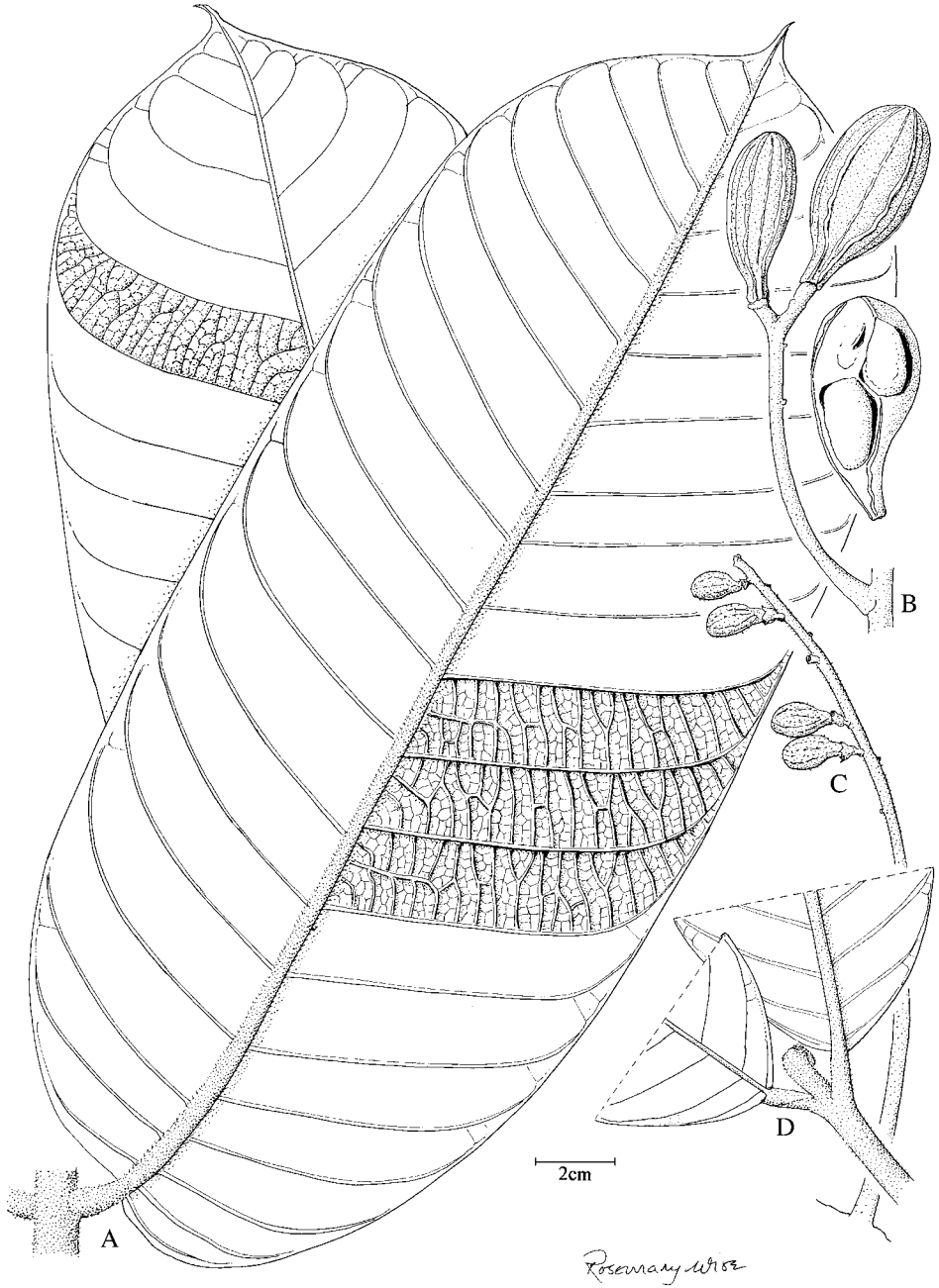


FIG. 43. *Guarea reticulatovenosa* T.D.Penn. A, leaflet; B, infructescence and fruit section; C, young infructescence; D, leaf apex with dormant bud. (A, B, *Forero et al.* 7202; C, D, *Franco et al.* 1302).

Colombia, Department Chocó, Municipio San José del Palmar, valley of R. Torito (affluent of R. Habita) [NW0476], 850–1000 m altitude, fr., iii 1980, E. Forero, R. Jaramillo, J. Espina & P. Palacios 7202 (holo MO).

Young shoots coarsely tomentose. *Leaves* pinnate with a terminal bud, exact length not known, but probably 40–50 cm long; petiole not seen, rhachis semiterete, at least 30 cm long (incomplete), 6–8 mm diam., densely golden pubescent; petiolule 1.2–1.5 cm long, swollen, densely pubescent, incomplete leaf with 2 pairs of leaflets. *Leaflets* opposite, 34–48 × 11.5–14.5 cm broad, broadly oblong to slightly oblanceolate, apex obtusely cuspidate to acuminate, base acute, obtuse or rounded, coriaceous and bullate, conspicuously reticulate-venose, upper surface glabrous, lower surface coarsely golden-pubescent on midrib and veins, hairs intermixed with some minute red papillae, not glandular-punctate or -striate; venation eucamptodromous in the lower two thirds, brochidodromous in the upper third, midrib slightly sunken, secondaries 23–26 pairs, shallowly ascending, slightly arcuate and ± parallel, short intersecondaries present, tertiaries oblique and parallel, numerous and very prominent on the lower surface (bullate); higher order reticulum evident on both surfaces. *Inflorescence* cauliflorous, 18–20 cm long, a slender panicle with very short lateral branches, shortly pubescent; pedicel (in specimens with young fruit) 2–3 mm long. *Flowers* not seen. *Capsule* c.5 × 2.5 cm, broadly oblong, apex obtuse to rounded, tapering at the base into a stout stipe c.1 cm long, 4-valved, valves shallowly and irregularly longitudinally 3-ribbed, ribs anastomosing in upper half, finely puberulous, pericarp c.2 mm thick, apparently fleshy, valves slightly constricted between the seeds, 2 superposed seeds in each valve, c.2 × 1.1 cm long, slightly plano-convex, completely surrounded by a thin fleshy sarcotesta. *Seed coat* thin and fleshy.

Field characters. A little-branched treelet to 7 m high, cauliflorous, fruit maturing red, the seed with a yellowish sarcotesta. Fruiting in March.

Distribution and ecology. In wet lower montane rain forest between 850 m and 1100 m altitude, on the eastern slopes of the western Cordillera of the Andes, in the department of Chocó, Colombia.

Collections examined. COLOMBIA. **Chocó:** vereda 'La Holanda' (NW0476), Franco *et al.* 1302 (COL, MO).

The strongly bullate reticulate leaflets of *Guarea reticulatovenosa* are similar to those of *G. sprucei* (Amazonian Brazil), but somewhat larger and with more secondary veins. It also differs from *Guarea sprucei* in its cauliflorous inflorescence, flowers with 4-locular ovary, and the broadly oblong fruit narrowed to a stout stipe at the base, and fruit valves with 3 very shallow anastomosing ribs.

- 63. *Guarea rhopalocarpa*** Radlk., Bull. Herb. Boissier, Sér. 2, 5: 191 (1905); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 350 (1981). – Type: Costa Rica, Cartago, Tuis, fr., *Tonduz* 11306 (holo CR; iso G, GH, NY, P, US). **Figs 44, 56D.** *Guarea montana* Al.Rodr., Lankesteriana 6: 111 (2006), **syn. nov.** – Type: Costa Rica, Puntarenas, Cordillera de Tilarán, Monteverde Biological Station, San Luís, Buen Amigo, track to Veracruz, fl., *Z. Fuentes* 653 (holo INB; iso CR n.v., MO). For further synonymy see T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 350 (1981).

Abbreviated description. Young shoots and inflorescences minutely appressed puberulous, leaves with a terminal bud showing intermittent growth, leaflets up to 5 pairs, 12.5–24 × 4.8–9.5 cm, broadly oblong, oblanceolate or elliptic, chartaceous, glabrous above, but with numerous minute raised dots, lower surface puberulous to glabrous, secondary veins 9–12 pairs, inflorescence mostly cauliflorous or ramiflorous, 10–30 cm long, a densely-flowered pendulous spike, raceme or narrow panicle, petals 4–6, valvate, 9.5–14 mm long, minutely appressed puberulous, staminal tube 8–12.5 mm long, anthers 8–9, ovary 4–5(–6)-locular, locules with 2 superposed ovules, capsule 4–8 cm long, 3–4 cm broad, pyriform to ellipsoid, usually with a long tapering base, densely papillose-puberulous, 4–5-valved, valves broadly and shallowly 3-ribbed, ribs sometimes torulose, pericarp 6–10 mm thick, valves with 2 superposed seeds.

Distribution and ecology. Costa Rica and Panama to the frontier with Colombia, in lowland and montane rain forest up to 1500 m altitude.

Representative additional collections. COSTA RICA. **Alajuela:** Monteverde Reserve, Rio Peñas Blancas (NW1084), *Haber & Bello* 7904 (CR, K); Cantón de Upala, PN Guanacaste (NW1085), *Chavarria* 1198 (INB). **Guanacaste:** 3 km N of Santa Elena, Atlantic Exposure (NW1084), *Haber ex Bello* 3809 (CR); Estación Pitilla, La Cruz, Guanacaste National Park (NW1085), *Moraga* 346 (INB, K). **Heredia:** 9 km SW of Las Horquetas, Rio Sardinal (NW1084), *Grayum et al.* 5019 (MO). **Limón:** Braulio Carillo, beyond Rio Sucio (NW1083), *Gomez et al.* 22766 (K). **Puntarenas:** Monteverde, San Luis, Finca Buen Amigo (NW1084), *Fuentes* 267 (INB, K).

PANAMA. **Bocas del Toro:** Fortuna Dam Area, Oleoducto road (NW0882), *Churchill et al.* 4533 (K). **Chiriquí:** Quebrada Bonita, Fortuna Hydroelectric Project (NW0882), *Galdames et al.* 643 (K). **Cocle:** above El Cope (NW0880), *McPherson* 13624 (K). **Darien:** Pirre Massif, Alturas de Nique, above Cana mine (NW0777), *McPherson* 12192 (K). **Veraguas:** vicinity of Cerro Tute, (NW0881), *McPherson* 10671 (K).

COLOMBIA/PANAMA. **Chocó/Darien:** Alto de Nique, Cerro Pirre massif (NW0777), *Gentry et al.* 28693 (K).

Guarea montana is here reduced to synonymy. The characters used to justify separation in the protologue of *Guarea montana* are both minute and inconsistent. For example the ‘stipels’ present at the petiole apex of *Guarea rhopalocarpa* (which are actually a minute extension of the petiole margin) are rapidly caducous and therefore easily missed, and they are also present in some specimens cited as *G. montana* (e.g. *Alfaro* 57 (K)). Similarly the inflorescence of *Guarea montana* is said to be a narrow thyse, or sometimes apparently a raceme, differing from the ‘strictly racemose’ inflorescence of *G. rhopalocarpa*. Examination of a range of specimens of

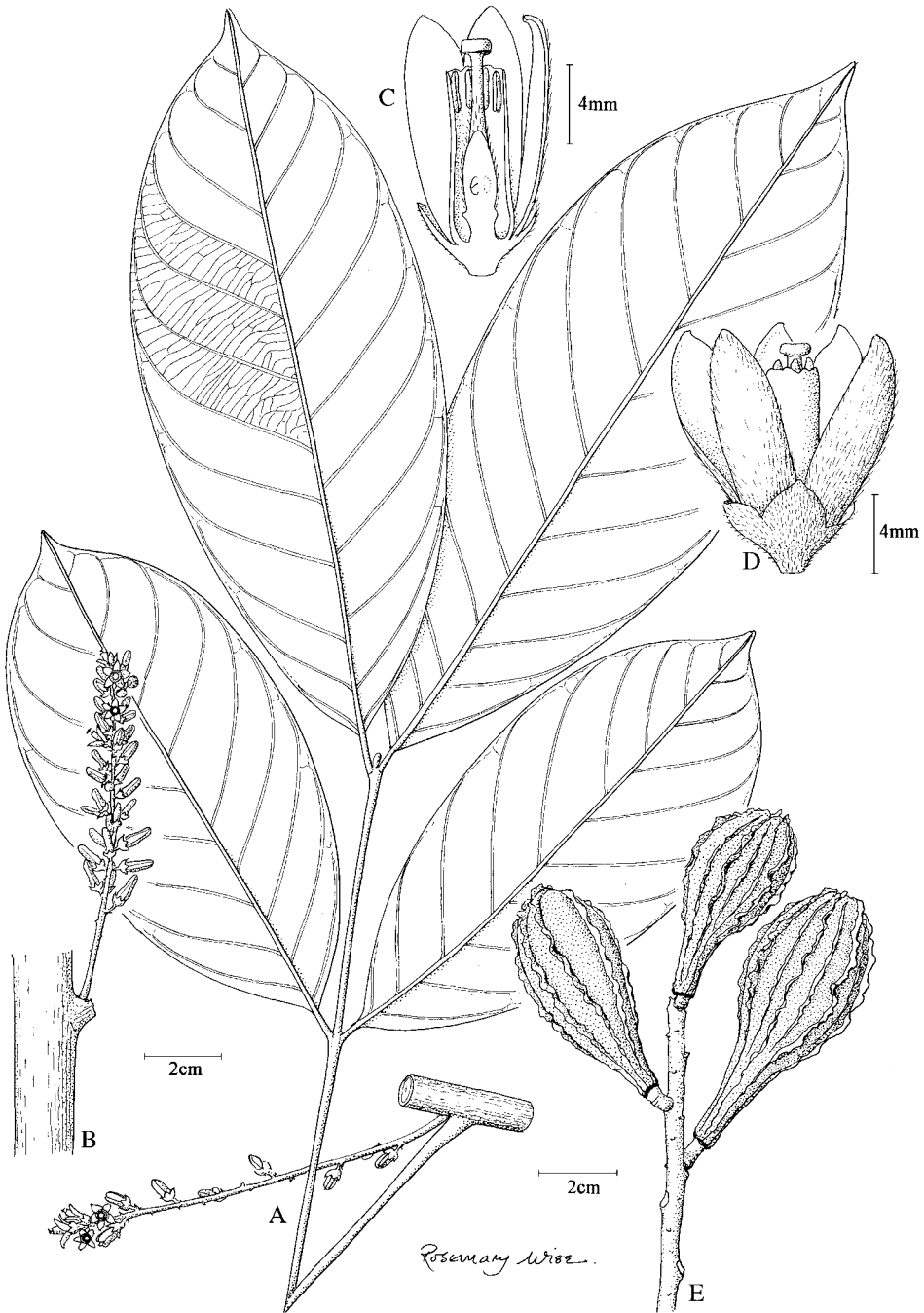


FIG. 44. *Guarea rhopalocarpa* Radlk. A, habit; B, inflorescence; C, half-flower; D, flower; E, infructescence. (A, Chacon 246; B-D, Neill 5116; E, Grayum et al. 5019).

Guarea rhopalocarpa reveals a complete gradation from spike to raceme to narrow thyrses. *Guarea montana* occupies the same geographical area and ecological and altitudinal zones and they flower at the same time of year.

64. *Guarea scabra* A.Juss., Bull. Sci. Nat. Géol. 23: 239 (1830); A.Juss., Mém. Mus. Hist. Nat. 19: 241, 285 (1831); T.D.Penn. in T.D.Penn. et al., Fl. Neotrop. 28: 304 (1981). – Type: Cayenne (French Guiana), fr., *Collector unknown* s.n. (holo P-JU; iso P). **Figs 45, 50D.**

Abbreviated description. Young shoots and inflorescences minutely appressed puberulous, leaves with a terminal bud showing intermittent growth, leaflets up to 6 pairs, 12.5–22.5 × 4–7.5 cm, elliptic, oblong or oblanceolate, chartaceous, glabrous, inflorescence ramiflorous (on smaller branches), or less frequently axillary, 3.5–20 cm long, a laxly-branched thyrses, the lower lateral branches to 10 cm long, petals 4–5, valvate, (7–)9.5–12 mm long, staminal tube (5.5–)7.5–9.5 mm long, 2–3 mm broad, anthers 8–9, ovary 4(–5)-locular, locules 1-ovulate, capsule 2–2.2 cm long, globose to broadly pyriform, slightly constricted between the seeds on drying, apex truncate, base rounded or tapered, 4-valved, smooth (see note below), minutely puberulous mixed with some longer pubescence, pericarp 2–3 mm thick, valves 1-seeded.

Distribution and ecology. Venezuela and the Guianas to central and western Amazonian Brazil and Peru, in non-flooded lowland rain forest.

Additional collections examined. VENEZUELA. **Amazonas:** Depto. Atabapo, between Duida and Marahuaca (NW0365), *Liesner* 25567 (K); Serranía de Tapirapeca (NW0164), *Marín* 1905 (K); Misión Río Mavaca (NW0265), *Stergios et al.* 15329 (K); Depto. Atabapo, Rio Purumane (NW0366), *Yanez* 495 (K).

GUYANA. Region Upper Takutu – Upper Essequibo, Kamoá Mts. (NW0158), *D. Clarke* 3132 (K); Kwitaro River (NW0358), *D. Clarke et al.* 6311 (K). Region Potaro-Siparuni, Mt. Ayanganna (NW0559), *H.D. Clarke et al.* 9662 (K); Kaieteur National Park, Potaro River (NW0559), *Gillespie et al.* 1377 (K); Gunn's, Essequibo River (NW0158), *Jansen-Jacobs et al.* 1912 (K).

SURINAM. Litani R. (NW0254), *Acevedo-Rodríguez et al.* 5753 (K); Tumuc Humac Mts., Talouakem (NW0254), *Acevedo-Rodríguez et al.* 5836 (K); Tumuc Humac Mts., Jari River (NW0254), *Acevedo-Rodríguez et al.* 6090 (K); Sipaliwimi, vicinity of Ulemari River (NW0254), *Evans & Peckham* 2859 (K), *Hammel et al.* 21662 (K).

FRENCH GUIANA. Saül (NW0353), *Mori & Gracie* 21165 (K), 23886 (K), *Mori & Pepper* 24300 (K), *Mori et al.* 24090 (K); Matiti, Point-Quadrat MAT (NW0552), *Prévost & Grenand* 4390 (K).

PERU. **Loreto:** Maynas, Iquitos-Nauta km 45 (SW0473), *Vásquez & Jaramillo* s.n. (K). **Pasco:** Palcazu valley (SW0968), *Hartshorn et al.* 2669 (K), 2769 (K). **San Martín:** Mariscal Cáceres, Tocache Nuevo (SW0876), *Schunke* 10061 (K).

BRAZIL. **Acre:** Município Mancio Lima, Parque Nacional Serra do Divisor (SW0773), *Daly et al.* 8884 (K). **Amapá:** Rio Falsino, Reserva INCRA (NW0151), *Campbell et al.* 14302 (K), 14806 (K); Município Macapá, Perimetral Norte (BR 210) (NW0153), *Daly et al.* 4002 (K); Município Macapá Riozinho (NW0153), *Mori & Cardozo* 17581 (K); Município Macapá, 154 km NW of Porto Grande (NW0153), *Rabelo et al.* 3086 (K, NY); Município Macapá, 7 km NW of Riozinho (NW0153), *Rabelo et al.* 3125 (K). **Amazonas:** Vila Bittencourt, Rio Japura (SW0169), *Amaral et al.* 505 (K); Manaus – Caracarái road km 97 (SW0257), *Cid et al.* 998 (K); Município Novo Airão, Área Indígena Waimiri Atroari (SW0161),

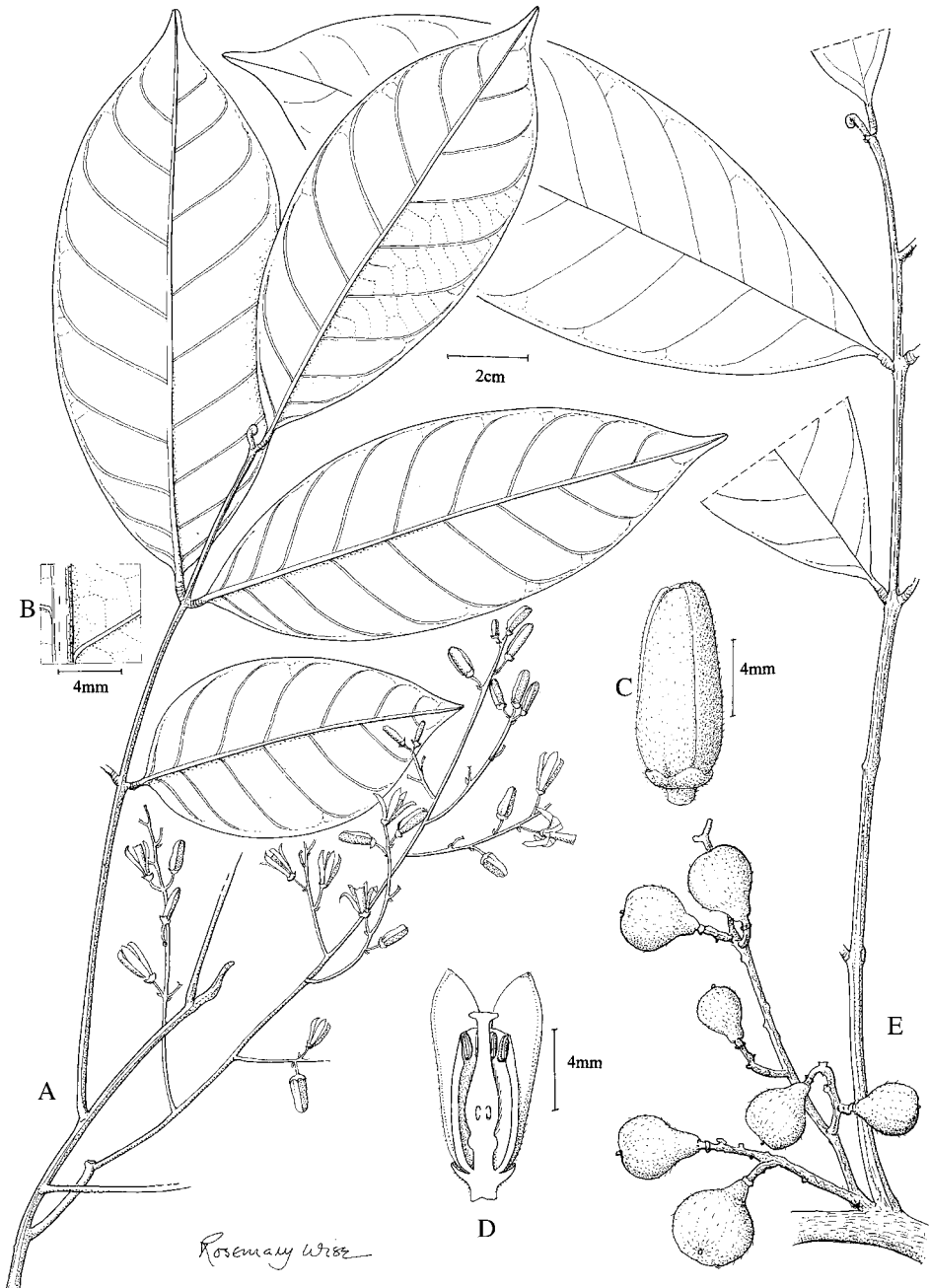


FIG. 45. *Guarea scabra* A.Juss. A, habit; B, enlargement of leaf undersurface; C, flower bud; D, half-flower; E, infructescence. (A, B, Acevedo-Rodriguez et al. 5753; C, D, Mori et al. 24090; E, Evans & Peckham 2859).

Milliken et al. 661 (K); Manaus, Reserva Florestal Ducke (SW0259), *Ribeiro et al.* 1901 (K). **Pará:** Ilha do Marajó, R. Anajos (SW0049), *Prance et al.* 30216 (K).

This species has a smooth capsule. It was incorrectly described as having a 3–4-ribbed capsule by Pennington in Pennington *et al.* (1981). This was due to an error in the labelling of a separate fruit collection.

65. *Guarea sphenophylla* Urb., *Symb. Ant.* 7: 242 (1912); T.D.Penn. in T.D.Penn. *et al.*, *Fl. Neotrop.* 28: 321, fig. 66 (1981). – Type: Haiti, Massif de la Hotte, Grand Goave, Morne Descassiers, fr., *Ekman* H9524 (neo S, designated by Pennington in Pennington *et al.* (1981: 322); iso K, NY). **Fig. 66D.**

For synonymy see T.D.Penn. in T.D.Penn. *et al.*, *Fl. Neotrop.* 28: 321 (1981).

Abbreviated description. Young shoots and inflorescences minutely appressed puberulous, leaves with a terminal bud showing intermittent growth, leaflets up to 6 pairs, 5–6.5 × 2.8–3 cm, oblanceolate, obovate or cuneiform, coriaceous, glabrous, venation eucamptodromous, secondaries 9–11 pairs, inflorescence axillary, 1–3 cm long, few-flowered, complete flowers not seen, anthers 8, capsule c.1.5 cm diam., globose, densely tuberculate-ribbed, sparsely to densely appressed puberulous, 3–4-valved, valves with 1–2 superposed seeds.

Distribution and ecology. Confined to Hispaniola (Haiti and Dominican Republic) on forested hills between 700 m and 1800 m altitude. No post-1981 collections have been seen.

66. *Guarea subsessilifolia* Al.Rodr., *Sida* 21(4): 2039 (2005). – Type: Costa Rica, San José, Turrubares, San Luís, Faldas del cerro Pelón, fl., *Rodríguez* 9613 (holo INB). **Figs 46, 61D.**

Young shoots coarsely pubescent at first, soon glabrous, smooth, greyish brown, 3–4 mm diam. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 1–2 mm long, semiterete, coarsely pubescent, rhachis up to 10 cm long, semiterete, coarsely pubescent to glabrous; petiolule c.2 mm long, swollen. *Leaflets* opposite, 1–3 pairs, 4.2–14.6 × 1.6–4.5 cm, oblanceolate or elliptic, apex narrowly acuminate, base acute or cuneate, chartaceous, upper surface with pubescent midrib, lower surface with scattered hairs along the midrib, otherwise glabrous, sparsely glandular-striate; basal pair of leaflets much reduced, 1–4.2 × 1–3.2 cm, broadly ovate to suborbicular with an asymmetric base; venation eucamptodromous to brochidodromous in the upper half, midrib sunken on the upper surface, secondaries 8–12 pairs, ascending, slightly arcuate and slightly convergent, intersecondaries absent, tertiaries oblique to horizontal. *Inflorescence* axillary, male 2–6 cm long, 8–35-flowered, female 1–3 cm long, 4–13-flowered, thyrsoid, coarsely pubescent to glabrous; pedicel 1.5–4 mm long. *Calyx* (male) 1–1.5 mm long, (female) 0.75–1 mm long, cup-shaped, shortly 4-lobed, sparsely pubescent. *Petals* 4, 5–5.5 mm long, valvate, strap-shaped, apex acute, appressed puberulous outside in the upper half.

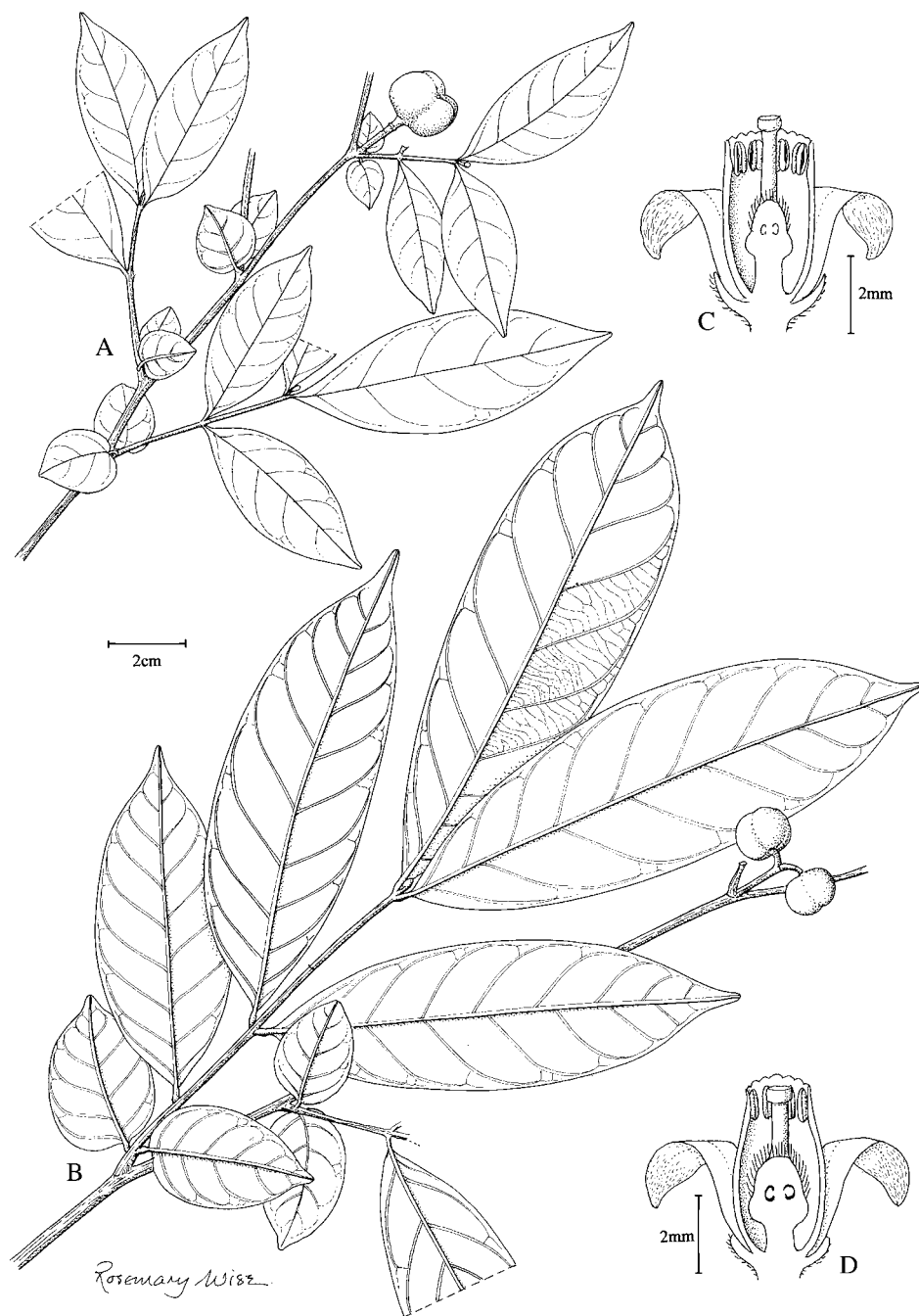


FIG. 46. *Guarea subsessilifolia* Al.Rodr. A, B, habit with fruit; C, half-flower (male); D, half-flower (female). (A, Zuniga et al. 376; B, Haber et al. 11670; C, D, adapted from Rodriguez (2005)).

Staminal tube 4–5 mm long, 1.5–2.5 mm broad, margin irregularly dentate, glabrous; anthers 8, 0.75–1 mm long, antherodes without pollen. *Nectary* c.1.5 mm long, a stout stipe expanded below the ovary. *Ovary* 4-locular, pubescent, locules 1-ovulate, style glabrous, style-head discoid. *Capsule* 1–1.5 cm long, 1–2 cm broad, \pm globose, apex rounded to truncate, base truncate, 4-valved, smooth, sparsely pubescent to glabrous, valves 1-seeded, pericarp 0.5–1 mm thick. *Seeds* 0.6–0.8 cm long, surrounded by a thin sarcotesta.

Field characters. Treelet to 4 m high, the bark with pink slash, flowers pinkish white, capsule maturing reddish green, seed surrounded by an orange sarcotesta. Flowering recorded in May, mature fruit in November.

Distribution and ecology. Species known only from wet montane forest on the Pacific slopes of Costa Rica (Puntarenas and San José), at 850 m to 1600 m altitude.

Collections examined. COSTA RICA. **Puntarenas:** Cantón de Puntarenas, Cordillera de Tilarán, Monteverde (NW1084), *Haber et al.* 11670 (INB, K). **San José:** Cantón Turrubares, SW spur of Cerro Turrubares (NW0984), *Grayum et al.* 10551 (INB); Cerro Turrubares, Zona Protectora (NW0984), *Jimenez* 534 (CR); Turrubares, San Luis, Faldas del Cerro Pelón (NW0984), *Rodríguez et al.* 9614 (BM); slopes of Cerro Bares, Cerros de Turrubares (NW0984), *Zúñiga et al.* 376 (INB, K).

This species has the floral and fruit structure of *Guarea glabra* and its relatives, but is easily recognised by the very short petiole and the pair of reduced basal leaflets. Reduced basal leaflets are widespread in the genus *Trichilia*, but have hitherto been unknown in *Guarea*.

67. *Guarea talamancana* Gómez-Laur. & M. Valerio, *Brenesia* 38: 147 (1992). – Type: Costa Rica, Limón, Suretka, La Pera [NW0982], fl., *Gómez-Laurito* 8820 (holo CR). **Fig. 61E.**

Young shoots densely golden tomentose, c.1 cm diam., indumentum persistent, eventually becoming glabrous, pale buff and suberous, with large pale lenticels. *Leaves* pinnate with a terminal bud showing intermittent growth, petiole 10–15 cm long, semiterete, golden-tomentose, rhachis to 55 cm long, semiterete to terete, tomentose; petiolule swollen, 3–6 mm long. *Leaflets* opposite, up to 6 pairs, 26–42 \times 11–18 cm, lowermost c.11 \times 7 cm, broadly oblanceolate, apex obtusely cuspidate, base acute, glabrous above, uniformly softly pubescent below with golden hairs, denser on midrib and veins, chartaceous; venation eucamptodromous, midrib sunken on the upper surface, secondaries 16–19 pairs, steeply ascending, slightly arcuate and convergent, intersecondaries absent, tertiaries oblique. *Inflorescence* cauliflorous and ramiflorous, c.2 cm long, a short spike, flowers subsessile. *Calyx* c.2 mm long, cup-shaped, margin shallowly and irregularly lobed, shortly pubescent outside. *Petals* 4, c.12 \times 2 mm, strap-shaped, apex acute, densely short-pubescent outside, glabrous inside. *Staminal tube* c.10 \times 2.5 mm, cylindrical, apex undulate, glabrous; anthers 8, c.2 mm long. *Nectary* a broad stipe c.1.5 mm long. *Ovary* 9–10-locular, locules with 1–2 superposed ovules,

densely golden-hirsute, style-head capitate. *Capsule* c.4 × 4 cm (immature), broadly pyriform, apex depressed, base obtuse, 8-valved, strongly 8-winged, the ribs c.1 cm deep and rounded dorsally, puberulous. *Seeds* not seen.

Field characters. Tree to 10 m high, trunk straight and cylindrical, with cauliflorous inflorescence.

Distribution and ecology. Known only from Costa Rica on the Caribbean slopes of the Cordillera de Talamanca, in rain forest up to 250 m altitude.

Collections examined. COSTA RICA. **Limón:** Talamanca, Suretka, La Pera (NW0982), *Gómez-Laurito* 8380 (CR); Talamanca, Sixaola, Gandoca, Rio Mile Creek (NW0982), *Herrera* 7656 (CR); Talamanca, Manzanillo, Finca de Bonilla (NW0982), *M. Valerio* 298 (CR); Talamanca, Reserva Indígena Bribri, Volio (NW0982), *Valverde et al.* 1157 (CR).

This species is distinct on account of the very large, softly pubescent leaflets, and the 8-valved, deeply ribbed fruit.

68. *Guarea trunciflora* C.DC. in A.DC. & C.DC., Monogr. Phan. 1: 571 (1878);
T.D.Penn. in T.D.Penn. et al., *Fl. Neotrop.* 28: 340 (1981). – Type: Poeppig &
Endlicher, *Nov. Gen. et Sp.* 3: 39, t. 245 (1843) (icon). **Figs 47, 50E.**
For synonymy see T.D.Penn. in T.D.Penn. et al., *Fl. Neotrop.* 28: 340 (1981).

Abbreviated description. Young shoots and inflorescences golden tomentose, twigs soon becoming suberised, leaves with a terminal bud showing intermittent growth, leaflets up to 7 pairs, 13–27 × 5–11 cm, elliptic, broadly oblong or oblanceolate, chartaceous, ± glabrous above, uniformly puberulous below with crisped pale whitish hairs intermixed with minute red papillae, secondary veins 13–18 pairs, inflorescence axillary or in the axils of fallen leaves, 3–20 cm long, a laxly-branched pyramidal thyse, lower branches spreading widely, to 6 cm long, petals 4(–5), valvate, 11–14 mm long, golden sericeous outside, staminal tube 8.5–10 mm long, ovary 4–5-locular, locules with 2 superposed ovules, capsule 3.5–5 cm long, 3–3.5 cm broad, pyriform, 4–5-valved, smooth or with faint longitudinal lines when dry, shortly velutinous, valves with 2 superposed seeds, pericarp 5–7 mm thick; seed c.1.7 × 1 cm, with plano-convex, superposed cotyledons.

Field characters. Tree to 30 m high. The mature capsule is red.

Distribution and ecology. Amazonian Colombia and Peru, southern Venezuela and Guyana to central Amazonian Brazil, in non-flooded lowland rain forest over clay or sand.

Additional collections examined. COLOMBIA. **Amazonas:** Araracuara, Rio Caquetá (SW0072), *Alvarez et al.* 784 (K). **Caquetá:** region of Araracuara (SW0072), *Restrepo & Matapi* 390 (NY).
VENEZUELA. **Bolívar:** Municipio Atures, Rio Parguaza (NW0667), *Fernandez* 303 (MO).
GUYANA. Upper Takutu-Upper Essequibo, Rewa River (NW0258), *D. Clarke* 3627 (K); Kaoma Mts. (NW0158), *D. Clarke* 5004 (K); Acarai Mts. 4 km S of Sipa River (NW0158), *D. Clarke et al.* 7117 (K), 7719 (K).

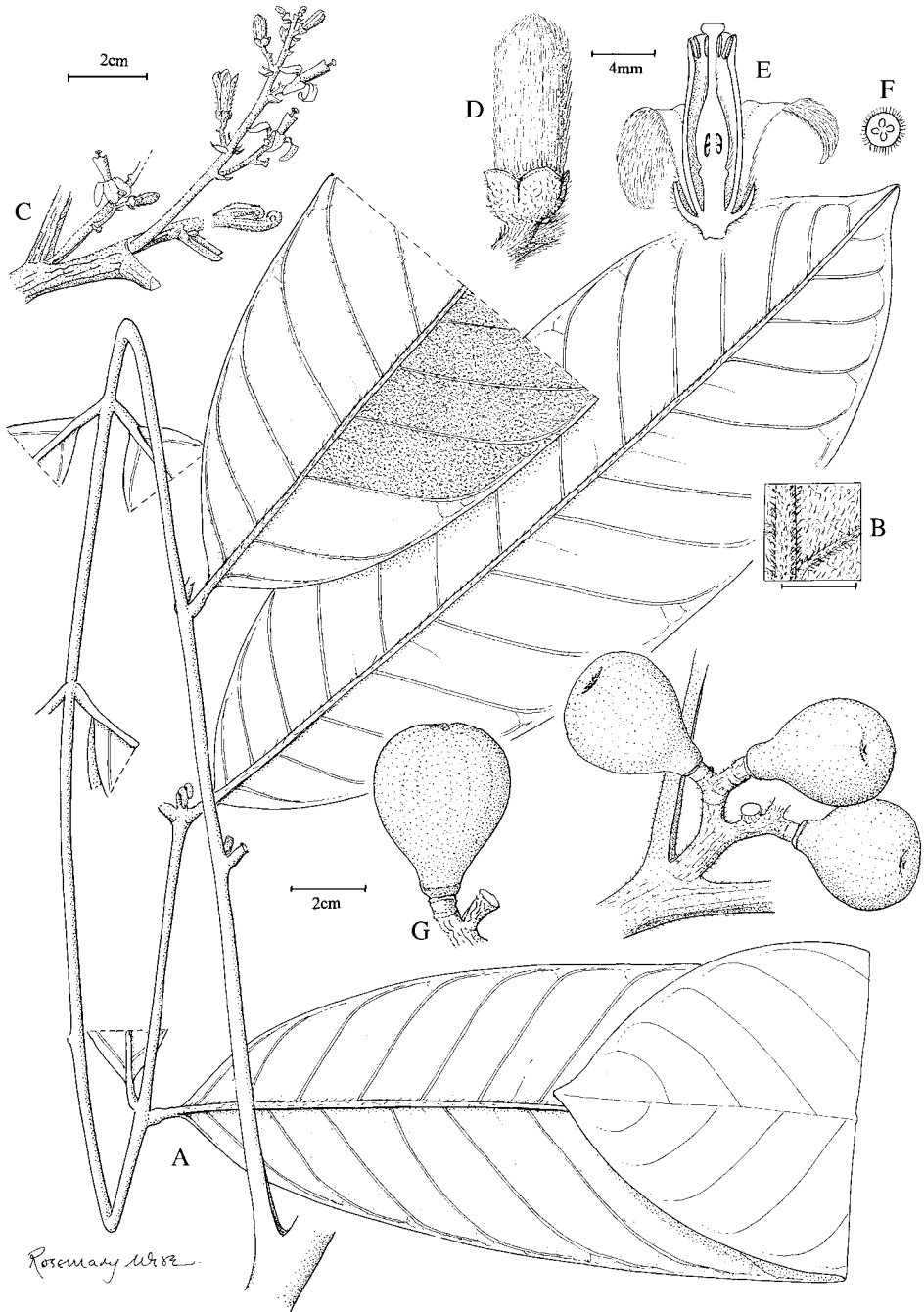


FIG. 47. *Guarea trunciflora* C.DC. A, habit; B, enlargement of leaf undersurface; C, inflorescence; D, flower bud; E, half-flower; F, cross-section of ovary; G, H, fruit. (A, B, G, H, Clarke, *D. et al.* 7719; C-F, Mori *et al.* 21325).

PERU. **Loreto:** Requena, 3 km E of Jenaro Herrera (SW0473), *Daly et al.* 6222 (K); Rio Nanay, Caserio Mishana (SW0373), *Foster et al.* 4906 (F, K); Iquitos, Puerto Almendras (SW0373), *Pennington & Criollo* 12413 (K); Requena, Quebrada de Curiyacu (SW0473), *Rimachi* 4322 (K); Rio Nanay, Puerto Almendras (SW0373), *Vásquez & Jaramillo* 10974 (K), 13655 (MO, QCNE); Maynas, Mishana (SW0373), *Vásquez et al.* 4004 (K).

BRAZIL. **Amazonas:** Município Novo Airão, Waimiri Atroari area (SW0161), *Milliken et al.* 495 (K), 631 (K); Distrito Agropecuario, Reserve 1501 (km 41) (SW0259), *Mori et al.* 21325 (K); Manaus, Ducke Reserve (SW0259), *Ribeiro et al.* 1620 (K), *Sothers & Silva* 411 (K), *Sothers & Pereira* 426 (K).

69. *Guarea venenata* T.D.Penn. in T.D.Penn. et al., *Fl. Neotrop.* 28: 346, fig. 73 (1981). – Type: Colombia, Amazonas, Trapecio Amazónico, fl., *Duque-Jaramillo* 2375 (holo COL). **Fig. 56E.**

Abbreviated description. Young shoots and inflorescences coarsely pubescent or tomentose, leaves with an apical bud showing intermittent growth, leaflets 3–9 pairs, 19–32 × 5.4–7.7 cm, oblong or narrowly elliptic, rarely oblanceolate, chartaceous, glabrous above, sparsely and coarsely pubescent below on the veins, with minute red papillae on the lamina, venation brochidodromous, secondary veins 25–30 pairs, ascending, straight and parallel, inflorescence cauliflorous, 1–3 cm long, racemose, petals 4, valvate, c.12.5 mm long, densely appressed pubescent outside, staminal tube c.8.5 mm long, c.2 mm broad, anthers 8, ovary 4-locular, locules with 2 superposed ovules, long-strigose, capsule unknown.

Distribution and ecology. Amazonian Colombia and extreme western Amazonian Brazil where it is an understorey treelet of lowland non-flooded rain forest. Not yet recorded from Peru but almost certainly to be found there. No post-1981 collections have been seen.

DOUBTFUL SPECIES

The following were treated as ‘Doubtful Species’ in the *Flora Neotropica* monograph (*Pennington et al.*, 1981), and in the absence of further information on their relationships they remain dubious. See *Pennington* in *Pennington et al.* (1981: 357–359) for further discussion.

Guarea apiodora Baillon

Guarea longifoliola C.DC.

Guarea lophos Vell.

Guarea macrobotrys Poepp. & Endl.

Guarea maynasiana C.DC.

Guarea sinuata Roemer

Guarea suberosa C.DC.

Guarea subsetulosa Harms

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MAPS

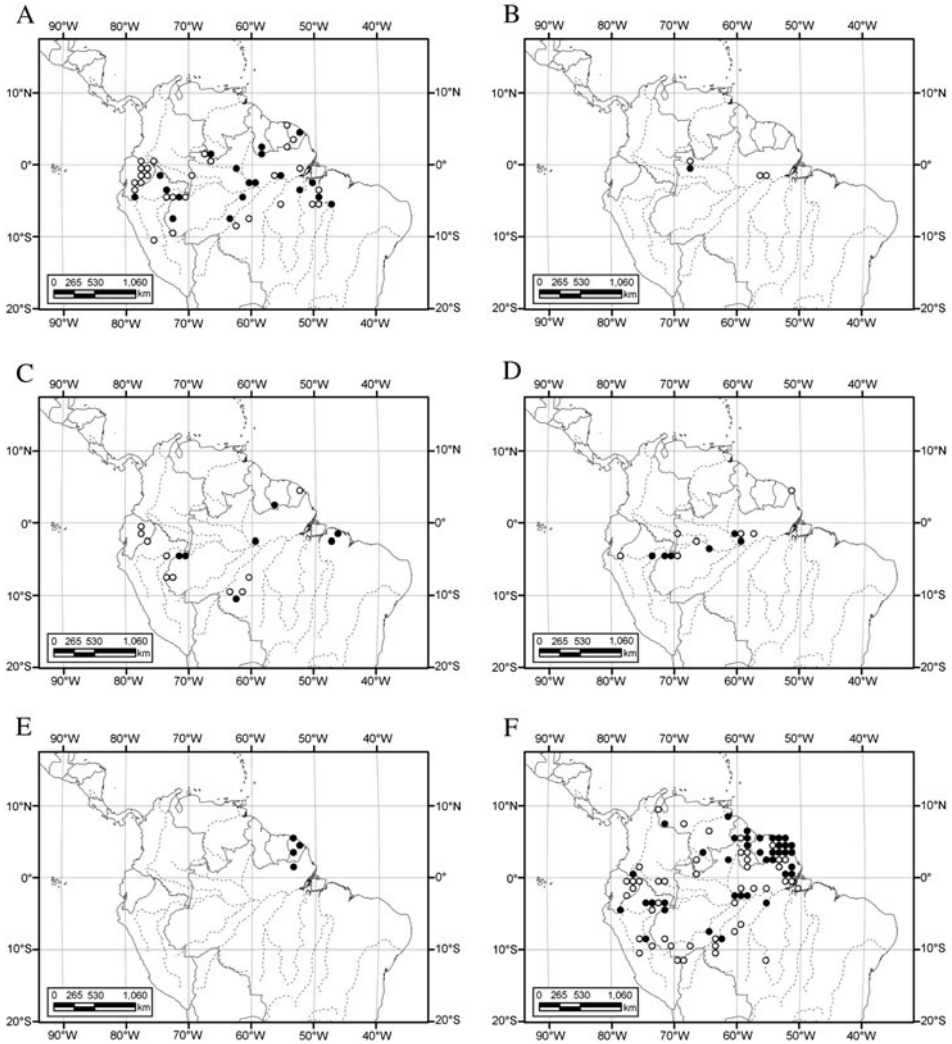


FIG. 48. Distribution of A, *Guarea silvatica* C.DC.; B, *Guarea sprucei* C.DC.; C, *Guarea carinata* Ducke; D, *Guarea cinnamomea* Harms; E, *Guarea michel-moddei* T.D.Penn. & S.A.Mori; F, *Guarea pubescens* (Rich.) A.Juss. subsp. *pubescens*. (A–D, F: Solid dots, distribution pre-1981, open dots new records 1981–2010. E: Total distribution to 2010).

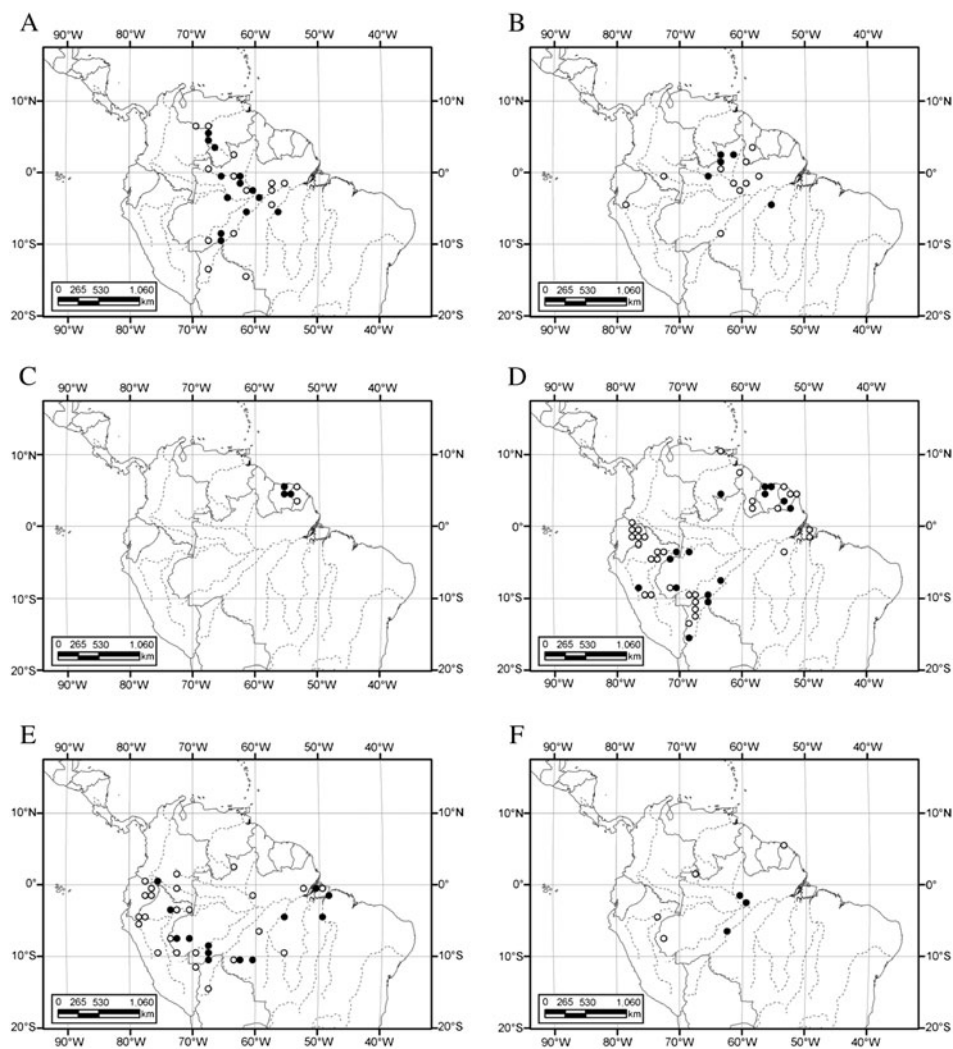


FIG. 49. Distribution of A, *Guarea pubescens* (Rich.) A.Juss. subsp. *pubiflora* (A.Juss.) T.D.Penn.; B, *Guarea velutina* A.Juss.; C, *Guarea costata* A.Juss.; D, *Guarea gomma* Pulle; E, *Guarea purusana* C.DC.; F, *Guarea convergens* T.D.Penn. (A–F: Solid dots, distribution pre-1981, open dots new records 1981–2010).

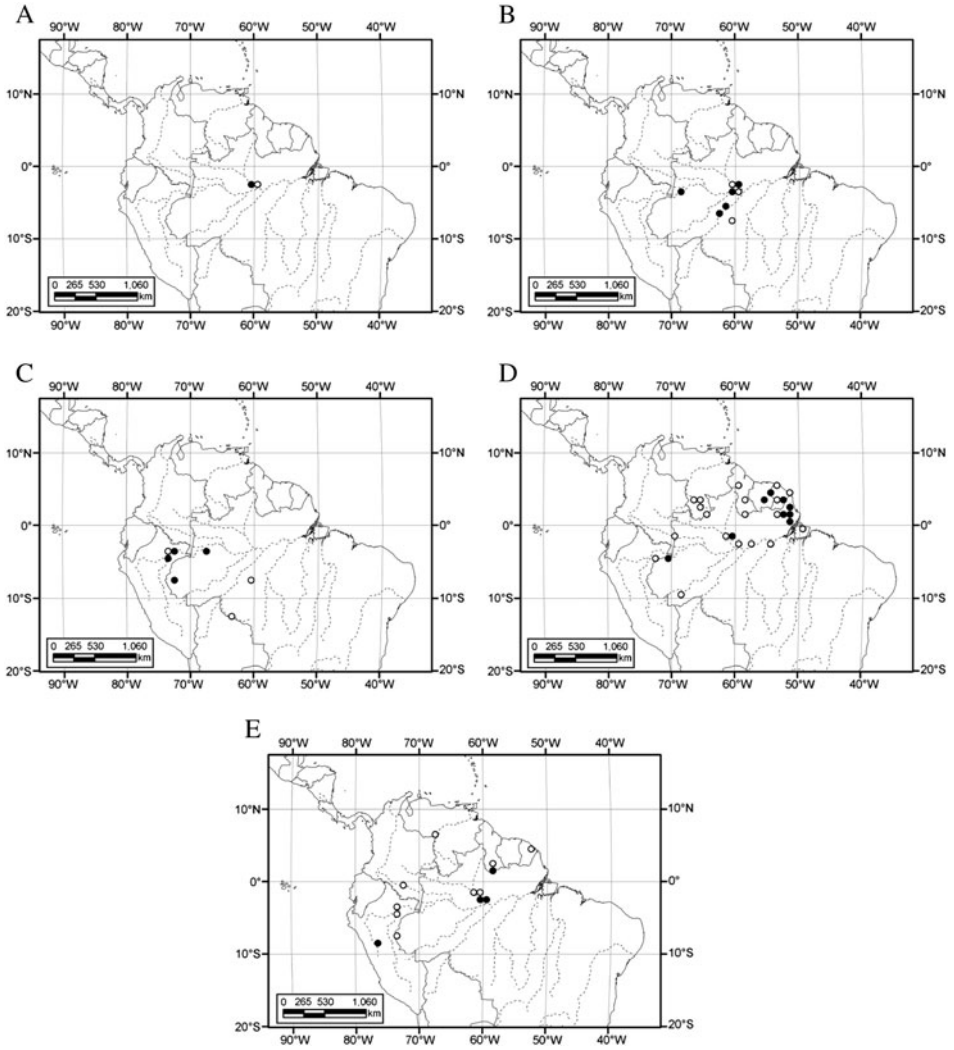


FIG. 50. Distribution of A, *Guarea crispata* T.D.Penn.; B, *Guarea humaitensis* T.D.Penn.; C, *Guarea juglandiformis* T.D.Penn.; D, *Guarea scabra* A.Juss.; E, *Guarea trunciflora* C.DC. (A–E: Solid dots, distribution pre-1981, open dots new records 1981–2010).

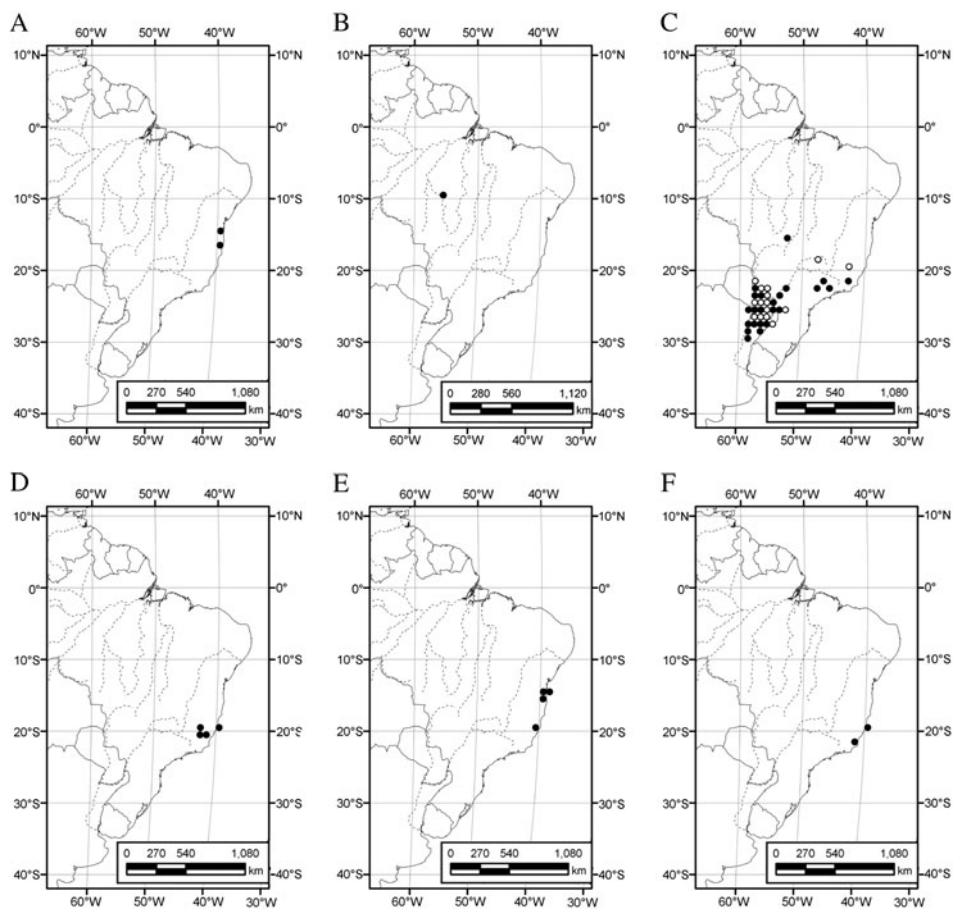


FIG. 51. Distribution of A, *Guarea anomala* T.D.Penn.; B, *Guarea zepivae* T.D.Penn.; C, *Guarea macrophylla* Vahl subsp. *spiciflora* (A.Juss.) T.D.Penn.; D, *Guarea pendula* R.S.Ramalho et al.; E, *Guarea blanchetii* C.DC.; F, *Guarea gracilis* T.D.Penn. (A, B, D–F: Total distribution to 2010. C: Solid dots, distribution pre-1981, open dots new records 1981–2010).

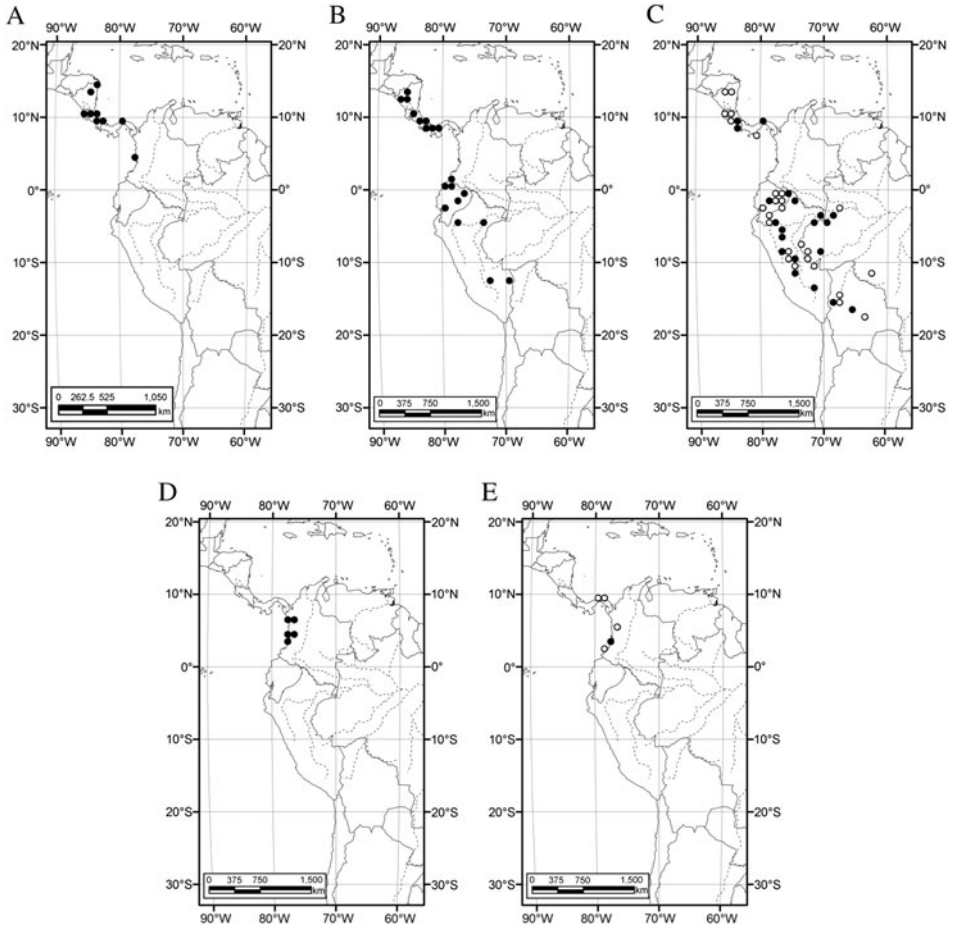


FIG. 52. Distribution of A, *Guarea gentryi* Coronado; B, *Guarea glabra* Vahl subsp. *microcarpa* (C.DC.) T.D.Penn.; C, *Guarea pterorhachis* Harms subsp. *pterorhachis*; D, *Guarea pterorhachis* Harms subsp. *submarginalis* T.D.Penn.; E, *Guarea caulobotrys* Cuatrec. (A, B, D: Total distribution to 2010. C, E: Solid dots, distribution pre-1981, open dots new records 1981–2010).

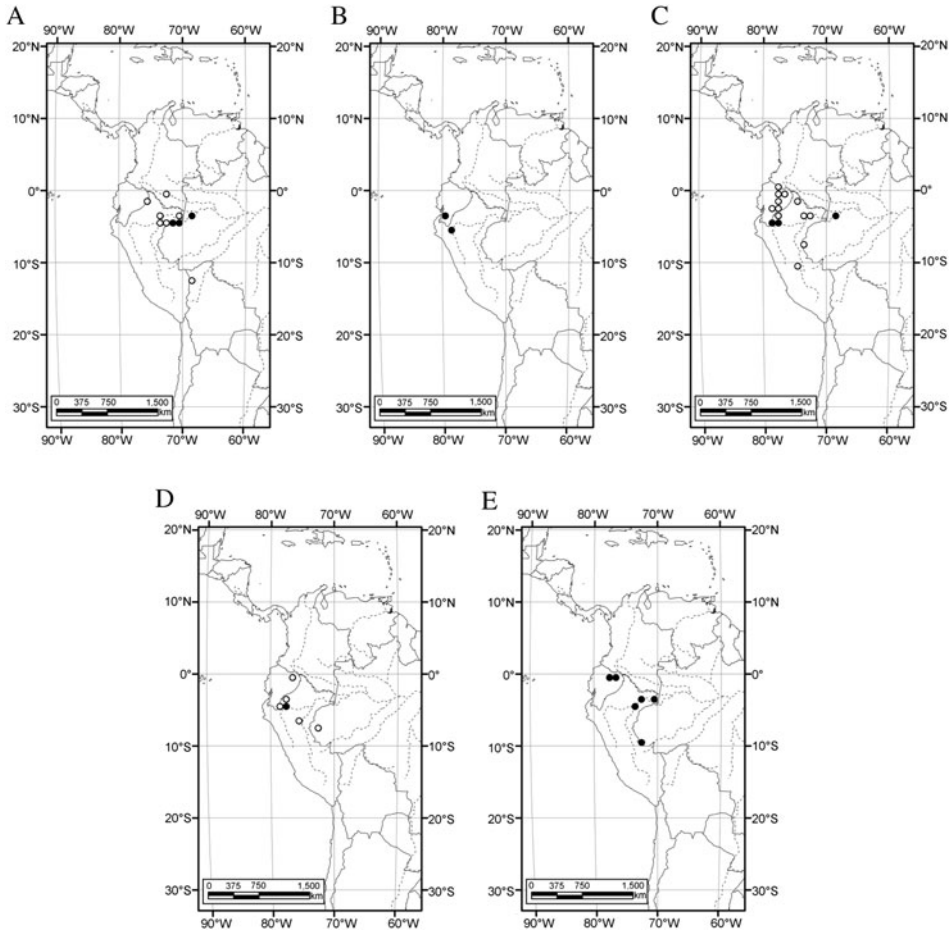


FIG. 53. Distribution of A, *Guarea cristata* T.D.Penn.; B, *Guarea subandina* W.Palacios; C, *Guarea guentheri* Harms; D, *Guarea carapoides* Harms; E, *Guarea ecuadoriensis* W.Palacios. (A, C, D: Solid dots, distribution pre-1981, open dots new records 1981–2010. B, E: Total distribution to 2010).

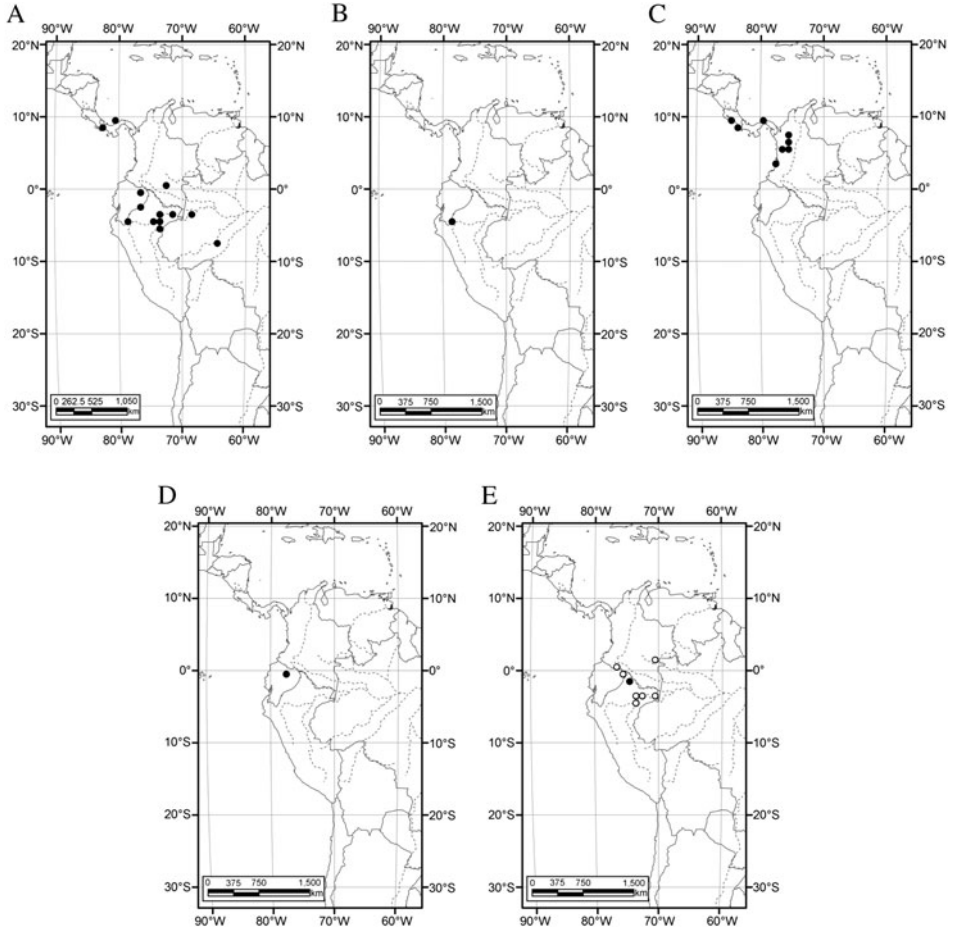


FIG. 54. Distribution of A, *Guarea fistulosa* W.Palacios; B, *Guarea riparia* W.Palacios; C, *Guarea pyriformis* T.D.Penn.; D, *Guarea persistens* W.Palacios; E, *Guarea fissicalyx* Harms. (A–D: Total distribution to 2010. E: Solid dots, distribution pre-1981, open dots new records 1981–2010).

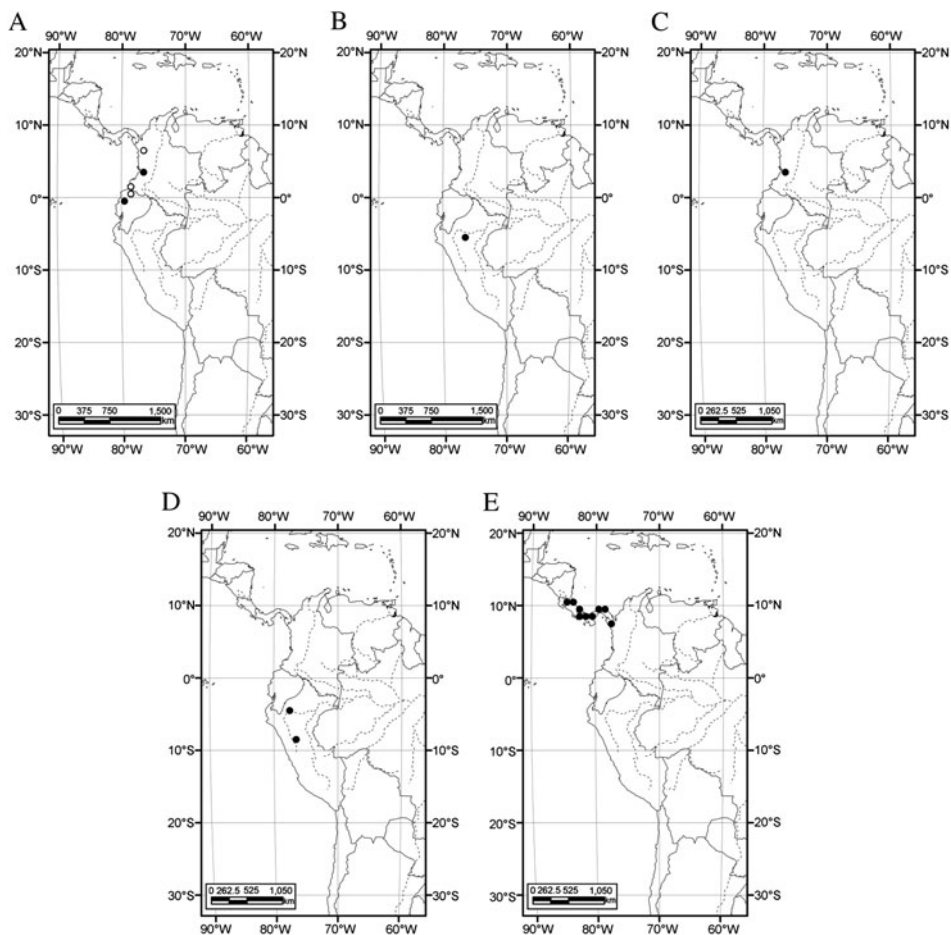


FIG. 55. Distribution of A, *Guarea cartaguenya* Cuatrec.; B, *Guarea casimiriana* Harms; C, *Guarea corrugata* Cuatrec.; D, *Guarea eriorhachis* Harms; E, *Guarea hoffmanniana* C.DC. (A: Solid dots, distribution pre-1981, open dots new records 1981–2010. B–E: Total distribution to 2010).

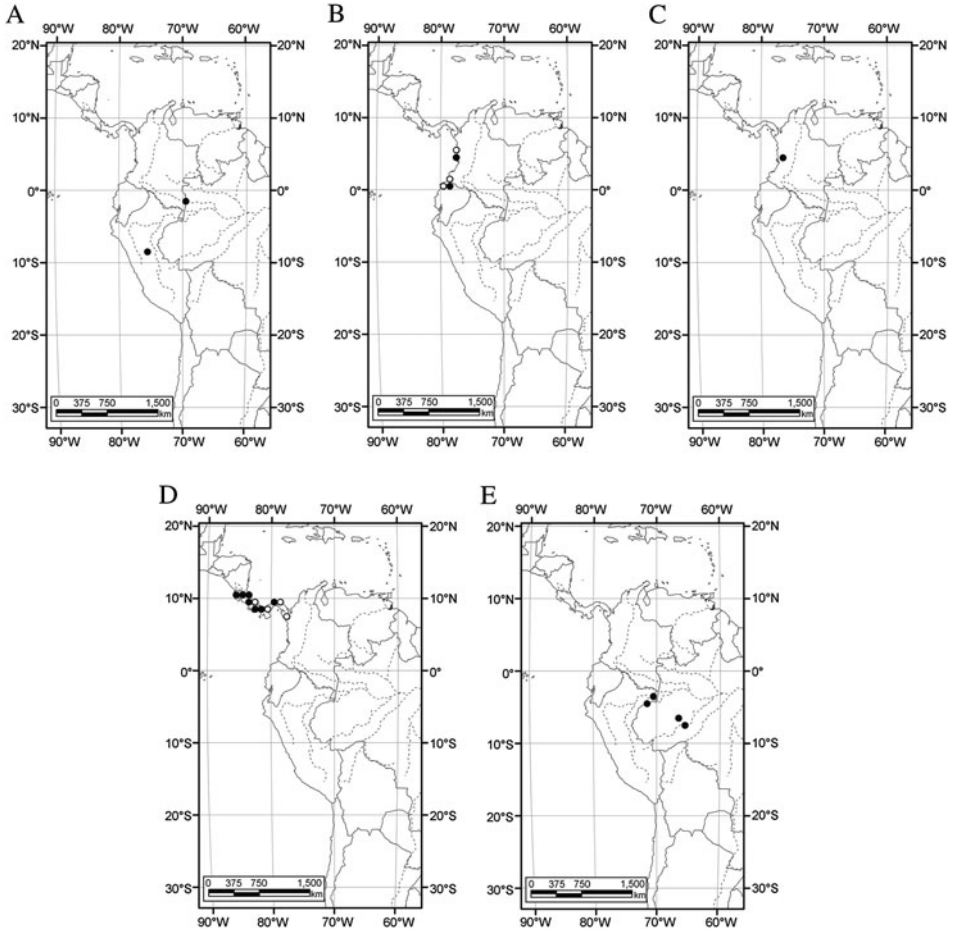


FIG. 56. Distribution of A, *Guarea lozanii* M.E.Morales; B, *Guarea polymera* Little; C, *Guarea reticulatovenosa* T.D.Penn.; D, *Guarea rhopalocarpa* Radlk.; E, *Guarea venenata* T.D.Penn. (A, C, E: Total distribution to 2010. B, D: Solid dots, distribution pre-1981, open dots new records 1981–2010).

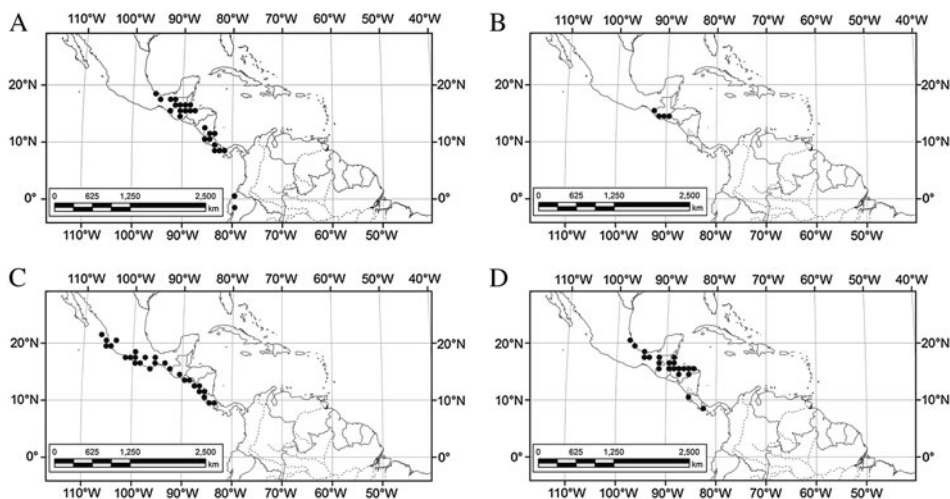


FIG. 57. Distribution of A, *Guarea bijuga* C.DC.; B, *Guarea luxii* C.DC.; C, *Guarea glabra* Vahl subsp. *excelsa* (Kunth) T.D.Penn.; D, *Guarea glabra* Vahl subsp. *tuerckheimii* (C.DC.) T.D.Penn. (A–D: Total distribution to 2010).

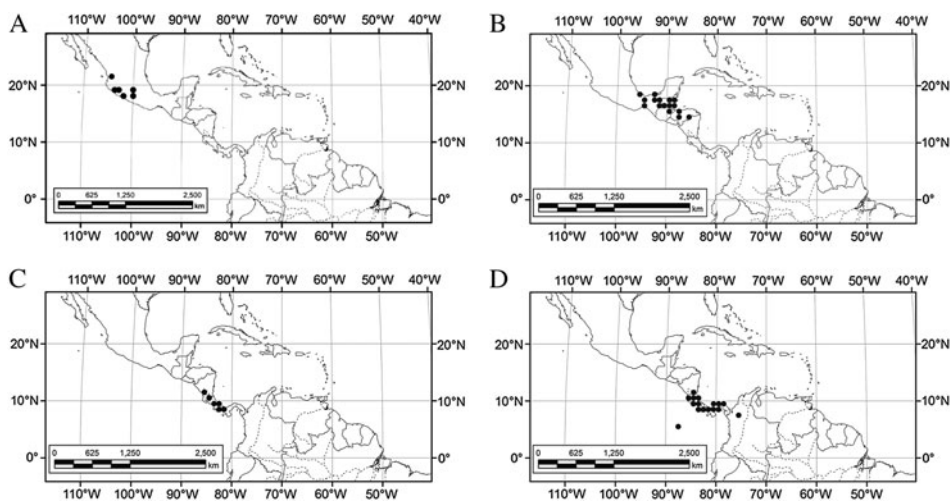


FIG. 58. Distribution of A, *Guarea glabra* Vahl subsp. *glabrescens* (Hook. & Arn.) T.D.Penn.; B, *Guarea glabra* Vahl subsp. *rovirosae* (C.DC.) T.D.Penn.; C, *Guarea tonduzii* C.DC.; D, *Guarea chiricana* Standl. (A–D: Total distribution to 2010).

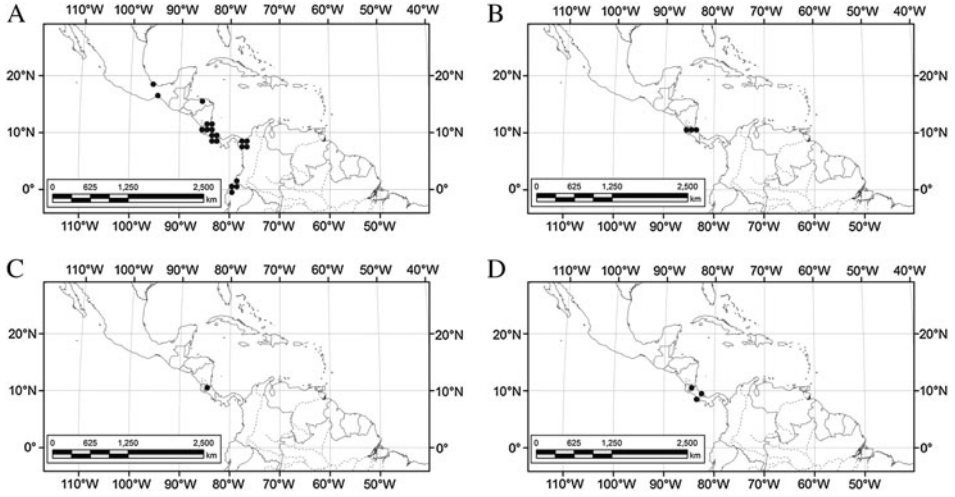


FIG. 59. Distribution of A, *Guarea bullata* Radlk.; B, *Guarea zarcoensis* Coronado; C, *Guarea tafaë-malekui* Al.Rodr.; D, *Guarea macrocalyx* Al.Rodr. (A–D: Total distribution to 2010).

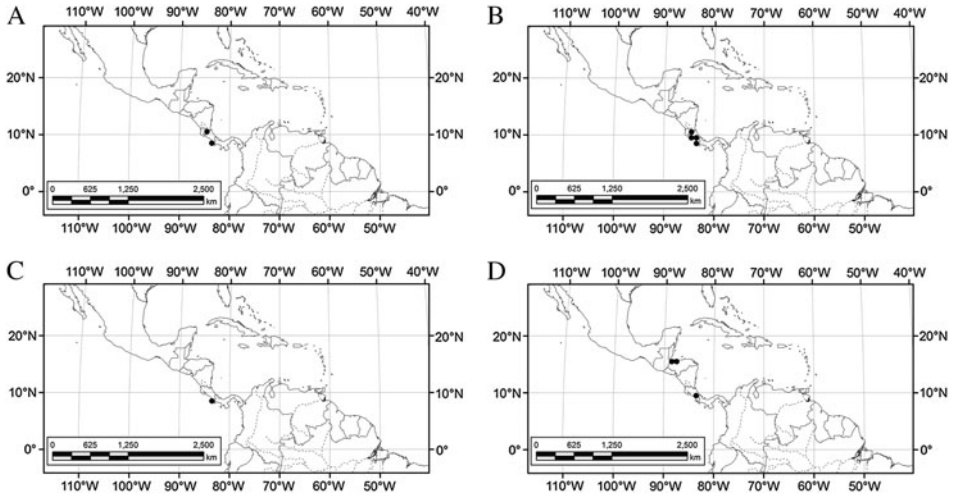


FIG. 60. Distribution of A, *Guarea aguilarii* Al.Rodr.; B, *Guarea constricta* Al.Rodr.; C, *Guarea corticosa* Al.Rodr.; D, *Guarea donnell-smithii* C.D.C. (A–D: Total distribution to 2010).

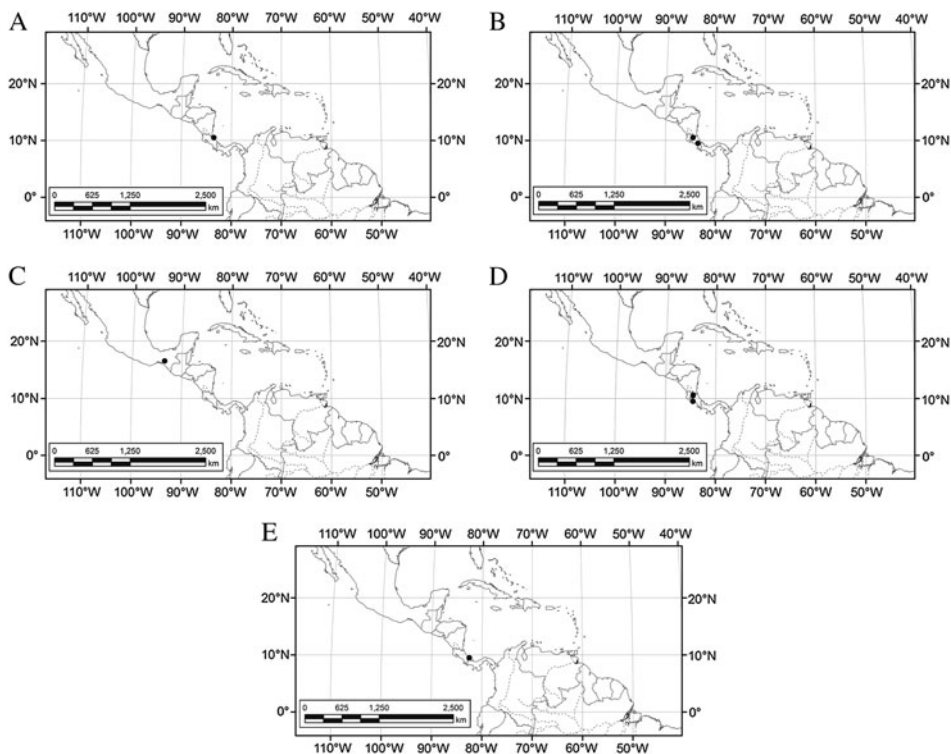


FIG. 61. Distribution of A, *Guarea grossa* T.D.Penn.; B, *Guarea inesiana* Al.Rodr.; C, *Guarea mexicana* Coronado; D, *Guarea subsessilifolia* Al.Rodr.; E, *Guarea talamancana* Gómez-Laur. & M.Valerio. (A–E: Total distribution to 2010).

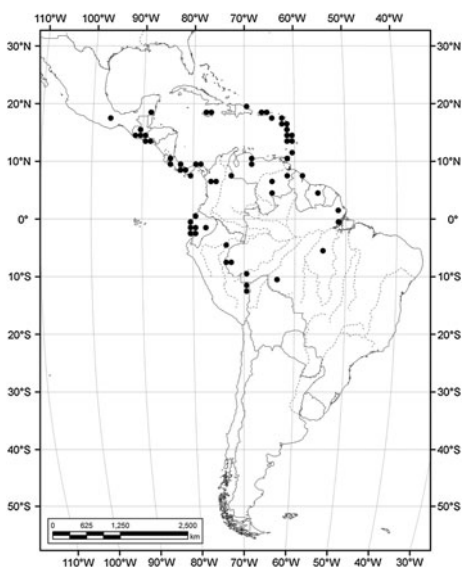


FIG. 62. Distribution of *Guarea glabra* Vahl subsp. *glabra*. Total distribution to 2010.

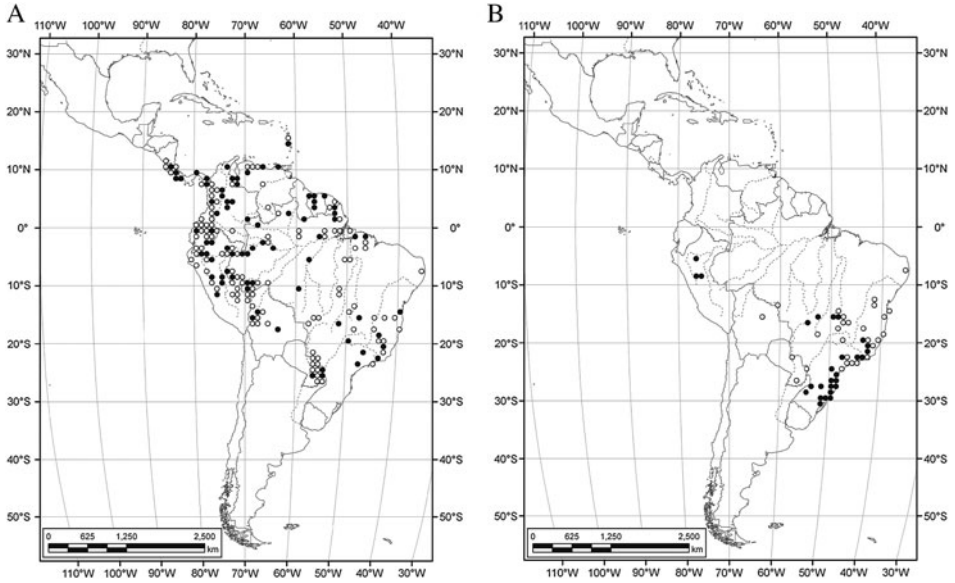


FIG. 63. Distribution of A, *Guarea kunthiana* A.Juss.; B, *Guarea macrophylla* Vahl subsp. *tuberculata* (Vell.) T.D.Penn. (A, B: Solid dots, distribution pre-1981, open dots new records 1981–2010).

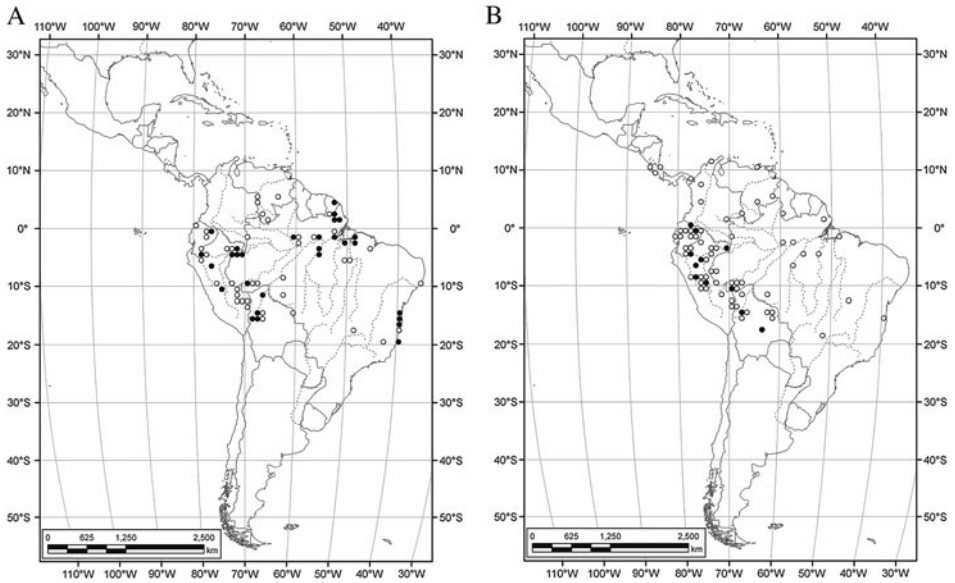


FIG. 64. Distribution of A, *Guarea macrophylla* Vahl subsp. *pachycarpa* (C.DC.) T.D.Penn.; B, *Guarea macrophylla* Vahl subsp. *pendulispica* (C.DC.) T.D.Penn. (A, B: Solid dots, distribution pre-1981, open dots new records 1981–2010).

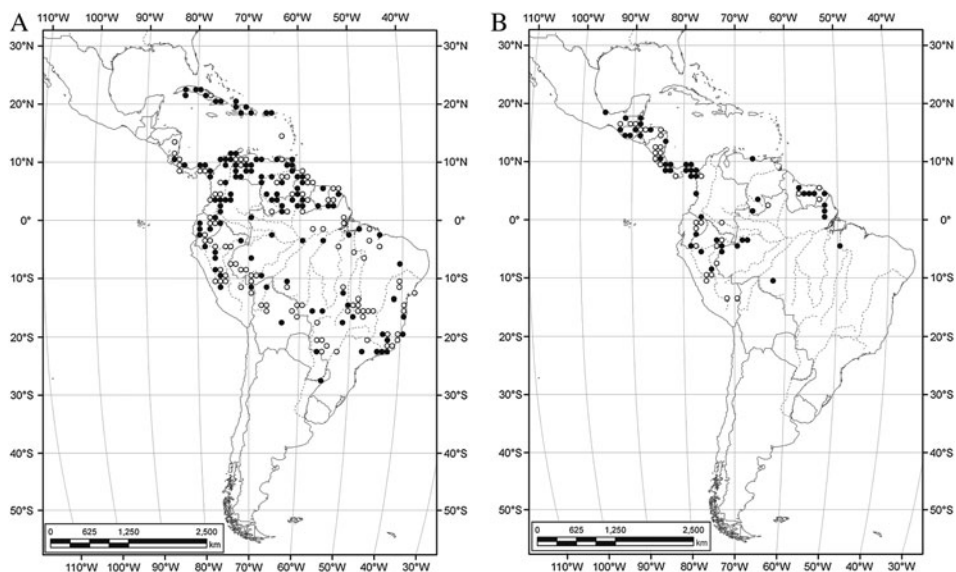


FIG. 65. Distribution of A, *Guarea guidonia* (L.) Sleumer; B, *Guarea grandifolia* DC. (A, B: Solid dots, distribution pre-1981, open dots new records 1981–2010).

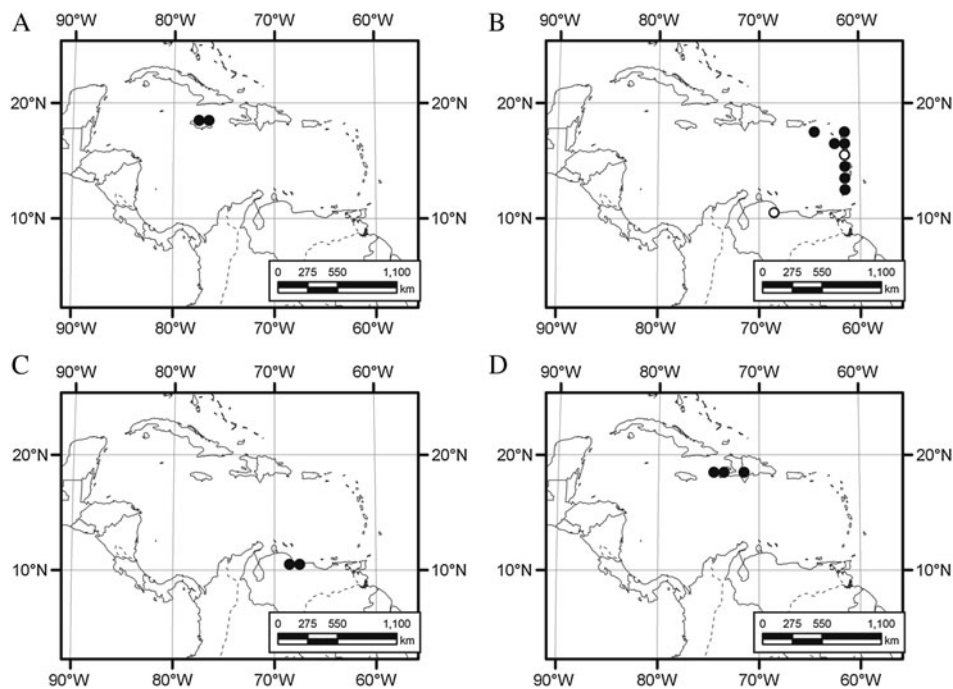


FIG. 66. Distribution of A, *Guarea jamaicensis* Proctor; B, *Guarea macrophylla* Vahl subsp. *macrophylla*; C, *Guarea megacostata* T.D.Penn.; D, *Guarea sphenophylla* Urb. (A, C, D: Total distribution to 2010. B: Solid dots, distribution pre-1981, open dots new records 1981–2010).

LIST OF EXSICCATAE

The List of Exsiccatae contains all collections made after 1980, including specimens not cited in the text above, plus a few earlier ones mentioned in the text, such as types.

Acevedo D et al. 150 (3); *Acevedo-Rodríguez & Cedeño* 7292, 7359 (1), 7475 (28a); *Acevedo-Rodríguez & China* 2195 (6a); *Acevedo-Rodríguez et al.* 150 (3), 150 (3), 1621 (34), 1706 (6c), 4978 (21a), 5678 (21a), 5753 (64), 5817 (40), 5836 (64), 5887 (21a), 5913 (40), 5986 (1), 6045 (37), 6090 (64), 7967 (21b), 8401 (21b), 9096 (10), 9654 (6a); *Acosta et al.* 1206 (8), 2030 (9); *Agostini G & T* 1629 (40); *Aguayo* 27, 51, 153, 166, 264, 284, 359, 361 (28c), 475 (10), 570, 574 (28c); *Aguilar* 312 (49), 476 (43), 488 (49), 708 (9), 790 (24), 1190 (6b), 1861 (12a), 2650 (sp.), 3083, 3437 (10), 6287 (8); *Aguilar & Gilbert* 3486 (8); *Aguilar & Hammel* 35 (3); *Aguilar et al.* 1985 (9), 2259 (4), 4172 (9); *Aguirre-Galviz* 922 (34?); *Aitken* 18197 (6a); *Alexander* s.n. (6a); *Alexiades & Byrne* 867 (28e), 870 (28d); *Alexiades et al.* 1021 (10), 184 (28a), 450 (28e); *Alfaro* 113 (4?), 4137 (6c); *Alfaro & Monro* 5537 (7); *Alfaro et al.* 57 (63), 63 (4); *Allen* 3376 (10), 5377, 5501 (36), 5804 (42), 5951 (12a); *Aluisio* 50 (47), 200 (64), 221 (68); *Alvarado* 22 (sp.), 22 (4?), 286 (10), 302 (1), 38 (38); *Alvarado et al.* 795 (6b); *Alvarengo & Perdigão* 935 (40); *Alvarengo et al.* 1273 (28e); *Alvarez et al.* 388 (42), 510 (10), 670 (42), 784 (68), 970 (10), 1866 (38), 2809 (58), 2809 (20); *Amaral* 1485, 1490 (40); *Amaral et al.* 1365 (1), 149 (21b), 304 (10), 463 (28e), 505 (64), 513 (1), 524 (28e); *Amorin et al.* 1279 (40); *Ancuash* 1508 (40), 20 (27), 30 (28d); *Andel van et al.* 10 (69?); *Anderson* 25 (40); *Anderson & Sternberg* 3471 (6a); *Anderson et al.* 1159, 1200 (40); *Andrle & Axtell* 9 (4); *Angulo* 139 (6c), 305 (sp.); *Angulo et al.* 45 (4?); *Aranda et al.* 67 (42), 3238 (6c); *Araquistain* 3135 (9), 3186 (40), 3769, 3795, 3802, 3817 (6b); *Araujo* 1480A (28b), 2063, 3381, 4309 (40); *Araujo et al.* 1056 (40), 1110, 4113 (28b); *Araya* 358 (8), 39 (40), 763 (10); *Araya et al.* 263 (9); *Arbo et al.* 5597, 7827 (40); *Arevalo* 520 (sp.); *Aristeguieta* 3182 (6a?); *Aristeguieta & Foldats* 1369 (40); *Aristeguieta & Huber* 318 (10); *Aristeguieta & Zabala* 6928 (40), 7078 (40); *Arnason & Lambert* 17033 (6f); *Asplund* 18762 (12a); *Assis et al.* 1071 (28b); *Assunção & Vicentini* 1 (55); *Assunção et al.* 328 (1), 809 (55); *Aulestia C* 942 (61); *Aulestia C et al.* 305 (44), 374 (44), 583 (44?); *Aulestia M* 2714 (10); *Aulestia M & Bainca* 3472 (12a); *Aulestia M & Gonti* 1976 (6c); *Aulestia M & Grefa* 185 (32); *Aulestia M & Omehuai* 3331 (1); *Aulestia M & Quihuinamo* 3197 (21a); *Aulestia M et al.* 1144 (12a), 3609 (12a); *Austin & Cavalcante* 4092 (28d), 4149 (39); *Avidel van et al.* 2668 (40); *Axelrod* 9001 (40); *Ayala* 1690 (57); *Ayala & Arevalo* 4299 (10); *Ayala et al.* 2515 (34); *Aymard & Delgado* 8075 (28d); *Aymard et al.* 6917 (28e), 9730 (28d); *Azevedo & Neto* 249 (28b).

Bagazo 188 (28e); *Baker* 11 (6b), 5904 (10), 5917 (37); *Baker et al.* 5944, 5951 (10), 5995, 6065, 6117 (42); *Balée* 1066 (28d), 3328 (40), 3404 (10); *Balée & Ribeiro* 1598 (40), 2742, 2796, 2848, 2892, 2923 (10), 293, 431 (40), 98 (28e); *Balick et al.* 2059 (6f), 2482 (4); *Ballestero* (49); *Balslev & Irvine* 4627 (28e); *Balslev et al.* 84692 (1), 84780 (41); *Bamps* 5379 (10); *Bang* 1373 (40), s.n. (28d); *Barbosa et al.* 8090 (34); *Barker & Thompson* 13 (28d); *Barretto* 13007 (40), 1386 (28b), 1440, 6334 (40), 9959 (10); *Barrier* 3375 (6a); *Barros* 1962 (28b); *Bartlett* 12210 (6f), 12321 (6f); *Bartlett & Lasser* 6635, 16997 (6a); *Bass* 357 (21a); *Basualdo* 1502, 1770 (28c), 1818 (10); *Basualdo et al.* 1412 (10); *Beard J* 229 (28a), 410, 463 (6a); *Beard P* 1165 (6a); *Beck* 6647 (40), 6886, 7335 (10), 7347 (5e?), 8128 (28e), 8292 (40), 9317 (10), 12244, 12740 (40), 18442 (28e); *Beck & Haase* 10162 (21b); *Beck & Seidel* 16731 (28e); *Beck et al.* 46 (1), 266 (39), 16442 (10), 20139 (28e), 20317 (28a); *Beck H T et al.* 281 (10); *Beechey* s.n. (6e), s.n. (6e); *Bello* 296 (4), 304 (4), 407 (10), 606 (42), 1252 (42), 1538 (63), 1631 (12a), 2044 (63), 2065 (8), 4621, 4958 (4); *Bello & Cruz* 4877 (7); *Bello et al.* 2740 (10); *Belshaw* 3147 (28d?); *Beltran* 32 (10); *Beltran & Foster* 709 (34); *Berendsohn et al.* 1603 (6a); *Berg et al.* BG 703 (42); *Berlin* 237 (35), 413 (21a), 562 (42), 3501 (42), 3581 (32); *Bermudez* 34928 (40); *Bernardi* 8/158 (5?), 18316,

20541 (28c), 7458 (40); *Berry et al.* 5421 (9); *Bertero* s.n. (6a); *Betancur et al.* 4970, 5070, 5084, 5124, 5215, 5430, 5440 (10); *Bigay & Irvine* 806 (40); *Blanchet* 2324 (30); *Blanco* 576 (21a); *Blum & Tyson* 2335 (8); *Bonpland* s.n. (6b); *Boom* 2625 (9), 4084 (28d), 9917, 10231, 10232 (40); *Boom & Mori* 1947 (37), 2012, 2070 (10), 2099 (37), 2100, 2105 (10), 2119 (42), 2133 (37), 2164, 2188, 2196 (10), 2215, 2219 (37), 2254 (10), 2269 (42); *Boom et al.* 7843 (12a), 8712 (50), 8771 (1); *Boon* 10056 (6a), 9587 (6a); *Bordas* 4394 (28c); *Bourdy* 1486, 1749 (10), 1823 (28d), 1918 (28e); *Bourgeau* 1197 (6b); *Box* 876 (28a); *Boyle* 917 (6c), 1263 (63), 1342 (9), 1394 (3), 1426 (9), 1429 (63?), 2464 (6c); *Boyle & Ezeta* 2797 (63), 2800 (3); *Boyle et al.* 230 (8), 1137 (10), 1139 (6c?), 1207, 1233 (63), 3896 (6a), 6888 (4); *Brade* 15436 (40); *Braga et al.* 19526 (40); *Brand & Gonzalez* 509 (9); *Brandbyge & Asanza* 30147 (42), 30391 (10), 30688 (17); *Brandbyge et al.* 30484 (10), 30569 (28e), 33516 (42); *Brant & Hazlett* 2881 (42), 2884 (51); *Breedlove* 10220 (60), 20245, 23899, 35320 (60), 56117 (sp.); *Breedlove & Almeda* 57994 (6d); *Breedlove & McClintock* 34211 (6d); *Breedlove & Smith* 21678 (60); *Breedlove & Thorne* 30774 (60); *Brenes* 4790 (7), 5832, 5852, 5883 (6c), 14316 (7), 20387 (4), 23132 (6c); *Breteler* 3660 (40), 4733 (21b), 4935 (10), 5150 (40); *Bridgewater & Ibanez* 458 (40); *Brito et al.* 17 (21a); *Britton et al.* 14448 (40); *Broadway* 205 (40), 3454 (28a), 4582 (6a); *Brooks* 12250 (40); *Brown* 6863 (6a), 17521 (6c); *Bruijn de* 1460, 1482 (40); *Brunner* 1157 (28c); *Brunner & Perez* 1192 (28c); *Buchtien* 1726 (12a), 1789 (10); *Bunting* 6449, 6788, 9476, 11618 (40); *Bunting & Alfonzo* 6451, 6941 (40); *Bunting & Arboleda* 8716, 8717 (40); *Bunting & Fucci* 8416 (40); *Bunting & Stoddart* 8957 (40); *Bunting & Trujillo* 11550, 11551 (40); *Bunting et al.* 7488 (40), 10895 (21a), 10964, 12055, 12408 (40); *Burger & Baker* 9561 (7), 9825 (63); *Burger & Gentry* 9113 (63); *Burger & Liesner* 7003 (8); *Burger & Matta* 4460 (63); *Burger & Visconti* 10212 (6c); *Burger et al.* 12462 (63); *Burgos* 31 (40); *Burkart* 14558 (10), 19398 (28c); *Bustamente* 277 (66); *Buttura* 273 (10), 487 (28b); *BW* 70 (37), 1665 (37), 1788 (42), 2304 (26), 4103 (64), 6677 (6a), s.n. (26); *Byron & Lima* 28116 (10).

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57777 (1), 57800 (40); *Silveira et al.* 1140 (10), 1278 (40), 1534 (10), 418 (28a), 460 (28d), 524 (1), 766 (28a); *Silverstone* 992 (40); *Silverstone-Sopkin & Paz* 6783 (28e), s.n. (10); *Simonis et al.* 238 (10); *Sintenis* 260, 1215, 1510, 2524, 2860, 4060 (6a), 4280 (40), 4396, 4441 (6a); *Skinner* s.n. (4); *Skutch* 1685 (4), 2665 (9), 3621 (7); *Smith A* 11 (4), 172 (4), 635 (4), 861 (22), 1686 (22), 4108 (7), 4111 (4), 1686 (22); *Smith A C* 2491 (40), 2715 (1), 2850 (10), 2914 (1), 3435 (40), 10233 (6a); *Smith D* 1877 (40), 1880 (40), 2060 (28e); *Smith D et al.* 1967 (28a); *Smith D N* 8440 (28a); *Smith D N & Garcia* 14137 (10), 14143 (12a); *Smith D N & Pretel* 7609 (10); *Smith D N & Salick* 8362 (42), 8384 (40); *Smith D N & Vásquez* 4704, 4738 (10); *Smith D N et al.* 7907, 7944, 8647, 8686, 13912, 14011 (10), 14021 (12a), 14116 (10), 14125, 14178 (28d), 14225 (28a), 14360 (40), 14361 (39); *Smith H* H407 (40); *Smith H H & G W* 532 (6a); *Smith J D* 2601 (6b); *Smith L B & Klein* 13130 (28b); *Smith N P* 13 (1); *Smith S F et al.* 962 (6c), 1063 (28d), 1407 (10); *Sobel et al.* 4788, 4789 (37); *Soejarto & Gennaro* 5699 (10); *Soejarto et al.* 4134 (36); *Solano* 61 (9); *Solomon* 5690, 6492 (40), 9116 (10), 13099 (12a), 19302 (9); *Solomon et al.* 6892 (28c); *Soria & Basualdo* 2198 (28c); *Sothers* 213 (55); *Sothers & Perreira* 426 (68); *Sothers & Silva* 411 (68), 456 (1), 659 (55); *Sothers et al.* 551 (28d); *Soto & Rojas* 1751 (8); *Sousa* 3287 (42); *Souza* 23 (40); *Souza & Silva* 33 (1); *Soza et al.* 97 (6b); *Sperling & King* 6440 (39); *Sperling et al.* 5958 (1), 6138 (10), 6406 (28d); *Sperry* 736 (9); *Spichiger & Encarnación* 1192 (17); *Spruce* 1686 (21b), 2240 (15), 2316 (1); *St Hilaire* s.n. (28c), s.n. (28b); *Ståhl* 6701, 6756 (4); *Ståhl & Andersson* 6290 (28e); *Ståhl & Cornejo* 6149 (28e); *Standley* 11228 (6b), 20134 (6a), 21297 (6b), 64991 (6a), 68562 (4), 79645 (6b), 84898, 85046 (5), 89145 (6b), 89260 (42); *Stannard et al.* 2617 (40); *Stehmann et al.* 2969 (28c), s.n. (40); *Stein* 1402 (40), 3431 (10); *Stein & McDade* 3334 (10); *Stein & Suarez* 3052 (10); *Steinbach* 1857 (28e), 5374 (40), 7227 (10); *Steinbach R F* 518 (12a); *Steinmann* 4362 (6e); *Stergios & Aymard* 9181 (28d); *Stergios & Stergios* 11316 (21b), 11408 (21b); *Stergios & Velazco* 13953 (28d), 14223 (42); *Stergios et al.* 9774 (21a), 15215 (28d), 15329 (64); *Stern et al.* 111, 182 (40), 213 (10), 1090 (6c); *Stevens* 11647, 22118 (6c), 23428 (sp.), 23712 (9), 23849 (10), 24312 (9), 24355 (54); *Stevens & Montiel* 17151 (6b); *Stevens et al.* 12953 (12a), 18932 (42), 20370 (6c), 21384 (12a), 21471 (42), 25383 (6d); *Steward et al.* 37 (68); *Steyermark* 36502, 45739 (4), 46644, 46867 (5), 47632 (42), 49239 (6d), 55850, 61516 (40), 61967 (10), 89059 (6a), 90726 (37), 101532 (21a), 107388 (40), 111544 (10); *Steyermark & Espinoza* 123802 (6a); *Steyermark & Liesner* 118502 (10); *Steyermark et al.* 101372 (10), 101950 (40), 119748 (10), 120419 (40), 125860, 125884 (21a), 126183 (40); *Steyermark J A & C* 95392 (59); *St Hilaire* s.n. (28c); *Stijfhoorn et al.* 877 (28a); *Stoffers et al.* 215 (40), 215 (40); *Strudwick et al.* 3419 (6a), 3855 (10); *Sucre* 484 (28b); *Sugden* 491 (42); *Sugden & Wint* 569 (42); *Sytsma & Andersson* 4553 (63); *Sytsma & Andersson* 4153 (40), 4716 (63); *Sytsma et al.* 2490 (sp.).

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Yanez 495 (64); *Young* 174, 177 (28a); *Young & León* 5015 (10); *Young & Salazar* 1024 (28a); *Yuncker et al.* 8442, 8706 (6d).

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Zardini & Guerrero 40111, 42693, 56815, 56815 (28c); *Zardini & Hellman* 48976 (28c), 49000 (10); *Zardini & Jara* 36521 (28c); *Zardini & Quintana* 53819 (28c); *Zardini & Tilleria* 37437 (28c); *Zardini & Velasquez* 11049, 11366 (10), 12042, 12177, 12209, 12466, 12564, 13219 (28c), 13319 (10), 13618 (28c), 13644 (10), 13761 (28c), 13795 (10); *Zardini & Velasquez* 13819 (28c), 13976 (10), 14252 (28c), 14256, 14606 (10), 14618 (28c), 14635, 15073 (10), 15111, 15113, 15122 (28c), 15125, 15173, 15177 (10), 15203, 15304, 15420, 15552, 15633, 15661, 15704, 15719, 15776, 16034, 16102, 17497, 18226, 18226, 18237, 18727, 20447, 20976, 21667, 21710 (10), 21735, 21955, 22120, 22570, 23804, 8926 (28c); *Zardini & Vera* 42606 (10); *Zardini & Zavala* 46739 (28c); *Zardini et al.* 11780, 15438, 3022 (28c); *Zarucchi* 2195 (28e); *Zarucchi & Balick* 1768 (41); *Zarucchi & Echeverry* 4718 (10); *Zarucchi et al.* 3020 (21b); *Zaruma* 297 (40), 443 (42), 590 (37), 683 (28d), 791 (37); *Zaruma & Arguello* 500 (28e); *Zaruma et al.* 35 (37), 48 (10), 135, 146 (40), 164, 166 (1); *Zuleta* 4 (40), 6 (28a), 10 (16), 128 (1), 28 (10), 312 (28a); *Zuniga* 524 (28e); *Zuniga et al.* 376 (66); *Zuzepczuk* s.n. (6d).

APPENDIX 1

List of Guarea DNA vouchers

G. anomala 30514 Brazil, *Mori & Benton* 12995 GenBank HE653770
G. bijuga 29879 Belize, *Pennil* 11 GenBank HE653766
G. blanchetii 30515 Brazil, *Jardim et al.* 225 GenBank HE653726
G. blanchetii 30516 Brazil, *Sant'ana et al.* 360 GenBank HE653727
G. blanchetii 30517 Brazil, *Kallunki et al.* 515 GenBank HE653728
G. bullata 25921 Mexico, *Cedillo Trigos* 31 GenBank HE653765
G. carapoides 30519 Peru, *Vásquez & Jaramillo* 20267 GenBank HE653730
G. carinata 25857 Ecuador, *Freire & Cerda* 149 GenBank HE653731
G. caulobotrys 30527 Panama, *McPherson* 11866 GenBank HE653746
G. chiricana 25922 Panama, *Foster* 2928 GenBank HE653767
G. cinnamomea 25859 Peru, *Pennington et al.* 17417 GenBank HE653732
G. costata 25860 French Guiana, *de Granville et al.* 8072 GenBank HE653733
G. cristata 30520 Peru, *Vásquez & Jaramillo* 4609 GenBank HE653734
G. cristata 30521 Colombia, *Duivenvoorden et al.* 2766 GenBank HE653735
G. ecuadoriensis 30522 Ecuador, *Palacios* 3193 GenBank HE653736
G. fissicalyx 25861 Peru, *McDaniel & Rimachi* 23667 GenBank HE653737
G. fistulosa 25871 Peru, *Revilla* 3668 GenBank HE653748
G. gentryi 30518 Colombia, *Fuchs & Zanella* 22361 GenBank HE653764
G. glabra subsp. *glabra* 25929 El Salvador, *Martinez* 694 GenBank HE653761
G. glabra subsp. *microcarpa* 25934 Peru, *Wurdack* 2127 GenBank HE653762
G. glabra subsp. *microcarpa* 25936 Ecuador, *Thomsen* 58825 GenBank HE653763
G. gommea 25862 Ecuador, *Baker* 5917 GenBank HE653738
G. gracilis 30523 Brazil, *Oliveira* 344A GenBank HE653739
G. grandifolia 3819 Peru, *Pennington* 10093 GenBank HE653725
G. guentheri 25864 Ecuador, *Toasa & Tirado* 8731 GenBank HE653740
G. guidonia 30524 Ecuador, *Pabón et al.* 296 GenBank HE653741
G. jamaicensis 25866 Jamaica, *Goodfriend* s.n. GenBank HE653758
G. kunthiana 25967 Peru, *Pennington & Daza* 16807 GenBank HE653759
G. luxii 25943 El Salvador, *Monterrosa et al.* 186 GenBank HE653769
G. macrocalyx 33283 Costa Rica, *Kernan* 1214 GenBank HE653742
G. macrophylla 25870 Paraguay, *Zardini & Zavala* 46739 GenBank HE653729
G. michel-moddei 30526 French Guiana, *Cremers & Gautier* 11959 GenBank HE 653745

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