FROM MORPHOLOGICAL NIGHTMARE TO MOLECULAR CONUNDRUM. PHYLOGENETIC, EVOLUTIONARY AND TAXONOMIC STUDIES ON *GUATTERIA* (ANNONACEAE).

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VAN MORFOLOGISCHE NACHTMERRIE TOT MOLECULAIR MYSTERIE.
FYLOGENETISCHE, EVOLUTIONAIRE EN TAXONOMISCHE STUDIES MET BETREKKING TOT *GUATTERIA* (ANNONACAEAE).

(met een samenvatting in het Nederlands)

PROEFSCHRIFT

ter verkrijging van de graad van doctor aan de Universiteit Utrecht op gezag
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door

ROY HUBERTUS JOHANNES ERKENS

GEBOREN OP 6 JANUARI 1976 TE MAASTRICHT

Promotor:	Prof. Dr. P.J.M. Maas
Co-promotor:	Dr. L.W. Chatrou

Geer nump 't later toch neet mèt, ’n eederein dee dat wel wèt.
En eeder jaor, zeet mer gerös, daan lik de breef van de belasting in de bös.
De wereld is neet laank meh roond, dee good kin lache is gezoond.
En noe alleh dreij daog drop oet, al mèt 'n trommel of 'n ratel en 'n toet.

(1960, Dreij daog d'r op oet, M. Niël)

Aan mijn ouders

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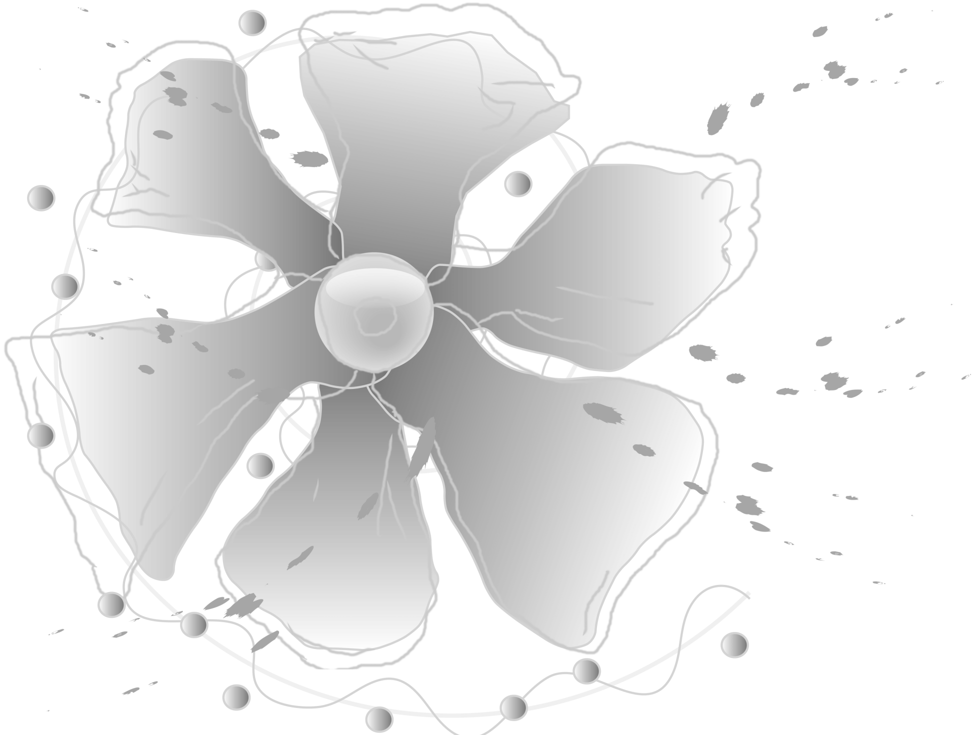


1 INTRODUCTION

Scientists estimate that the earth is currently inhabited by c. 10 million different types of organisms (also sometimes called "species"; Wilson, 2000), but some estimates are as high as 40 million. This means that at best 20% of all biodiversity has been identified and named (c. 2 million; 1.5 million animals (May, 1988), c. 300.000 plants (Willis & McElwain, 2002), c. 100.000 fungi (Hawksworth & Rossman, 1997) and c. 100.000 (?) prokaryotes and archaea (Ward, 2002)). However, as little as a few thousand species have been thoroughly studied in detail. This means that most of the world's organisms remain to be studied. The discipline within the science of Biology that is occupied with classifying all organisms on earth and tries to unravel the relationships between them is called systematics. Classifying biodiversity is non-trivial. Understanding (plant)diversity depends on having a good and reliable system of classification that serves as predictive reference system of information (Unknown, 2001).

Current day classification is based on the so-called binomial system introduced by Linnaeus in his *Species Plantarum* (1753), in which he replaced the antiquated Aristotelian system with the principles of classification used today. He classified the world into two kingdoms: animals and plants and introduced several hierarchical lower categories of ordering: class, order, genus, and species. To implement the discovery of bacteria and fungi, several new classifications were proposed but none of them survived. In 1969, the still widely used five-kingdom classification was proposed (Monera, Protista, Plantae, Fungi, Animalia). This classification featured several important improvements, one of them being the acknowledgement of two fundamentally different cell types: eukaryotic and prokaryotic. However, the last three decades it became clear that the five-kingdom division also had to be revised. As a result, the kingdom Protista has been further subdivided and the kingdom Monera is abolished. It was found that all cellular life can be divided into three primary lineages (domains), one eukaryotic (Eucarya, also called Eukaryota) and two prokaryotic (Bacteria and Archaea; Woese & Fox, 1977; Woese, 1987). Today the Linnean classification system comprises eight (main) levels: domain, kingdom, phylum, class, order, family, genus and species. The discussion on the classification of life has not ended yet and this classification is still very much "under construction."

Although researchers agree on the three domains of life, the exact relationship between these domains remains unclear (mainly because nobody knows how to root the tree of life). The reconstruction of relationships within the Bacteria and Archaea (Hugenholtz, 2002) is well on its way and the higher level relationships within the Eucarya are becoming increasingly clear. Fungi (Bruns & al., 1991; 1992; James & al., 2006), Animals (Halanych, 2004) and more specific the Plant kingdom are all investigated in so-called multi disciplinary Tree of Life (ToL) projects. For instance, the publications of the Angiosperm Phylogeny Group (APG, 1998; APG-II, 2003) have boosted an enormous amount of research and led to a fairly stable higher level classification of the Angiosperms that can be seen as authorative for the moment (see: http://www.mobot.org/MOBOT/research/APweb/). Because of the progress at the family level (and above), research is now shifting towards lower level phylogenetics, meaning the study of relationships between genera, species and even populations. This is an interesting trend. Understanding the relationships between groups of organisms at such a fundamental level will help us to understand the process of cladogenesis, the branching of the tree of life. This will eventually lead to a better understanding of the process of evolution. Understanding speciation is understanding the macro-evolutionary patterns over long periods of time because these large-scale patterns are inextricably caused by micro-evolutionary processes.

Where morphology was the main source of information for study in systematics some decades ago, its place now has been taken by molecular (sequence) data. These data are mostly used to construct a phylogenetic tree that shows the history of the diversification of clades. It is an explicit statement of the historical relationship between taxa. In other words such trees are hypotheses about the evolutionary history of a group derived from the data at hand (in contrast to the *true* unknowable evolutionary pathway: the phylogeny). Species-level phylogenetic trees are nowadays within reach and offer an enormous potential for investigating not only the general causes of speciation but also the rates of speciation within clades (Barraclough & Nee, 2001). Furthermore, phylogenetic trees have become essential tools for elucidating patterns of lineage diversification at the population level (Avise, 2000).

The research in the present thesis was started in order to reconstruct a phylogenetic tree of the Neotropical plant genus *Guatteria*, the largest genus in the family of Annonaceae. This research was conducted as part of the Annonaceae Research Project, a project initiated in 1984 at the Nationaal Herbarium Nederland – Utrecht branch. At the beginning of the project monographic studies of selected genera and morphological character analyses were the main focus. Nowadays the focus has shifted towards the reconstruction of molecular phylogenetic relationships of the genera and the investigation of associated character evolution. Especially at start-up, the project owed much to one of the pioneers of Annonaceae systematics: Robert Fries.

ROBERT E. FRIES

Klas Robert Elias Fries (figure 1) was born on the 11th of july 1876 in Uppsala, Sweden. He was born into a botanical family. His father, Thore Magnus Fries (1832-1913), was a botany professor at Uppsala University, and his grandfather, Elias Magnus Fries (1794-1878), had been Scandinavia's most famous mycologist (Buchwald, 1970). When he was 25 years old, he went on an extensive botanical exploration of the northern part of Argentina and the south of Bolivia as a member of the "Swedish expedition to Chaco and the mountain ranges" under leadership of Baron Erland Nordenskiöld (from May 1901 until May 1902). During this expedition, he investigated vegetation up until 6100 m above sea level. When he returned to Sweden he had collected many phanerogams, fungi and algae (Chardon, 1947). Research on these specimens at Uppsala University led in 1905 to his doctor's degree. His thesis was named "Zur Kenntnis der Alpinen Flora im nördlichen Argentinien"

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

(Unknown, 1966). After this, he held a teaching position for some time at Uppsala University. During this period he made his first trip to Africa as companion of Eric Conde Von Rosen in the years 1911-1912 (Chardon, 1947). Although they covered almost the whole continent his most important collections are from the vicinity of Lake Bangweolo and other parts of northern Zambia (at that time the British colony Rhodesia). The results of this expedition were published between 1914 an 1921 in a very extensive treatment called *Botanische Untersuchungen* (Parte I de *Wissenschaftliche Untersuchungen der Schwedischen Rhodesia-Kongo Expedition, 1911-1912*). In 1915 he was appointed director of the Hortus Bergianus (Professor Bergianus) and director of the Bergius foundation at Stockholm in 1915, a position he retained until his retirement in 1944 (Chardon, 1947; Unknown, 1966). In the years 1921-1922 he made a second trip to Africa (covering mainly Kenya and eastern Africa), this time with his brother Thore C.E. Fries (1886-1930), who had become a botany professor at Lund University.

He has written many publications on his trips to Africa and wrote groundbreaking treatments on the east African mountain vegetation (Jonsell & al., 1991). Next to this extensive work he contributed greatly to the flora of Central America, South America and the West Indies, especially to the knowledge of the family of Annonaceae. He for instance monographed the family in his 1959 contribution to Engler & Prantl's "*Die Natürlichen Pflanzenfamilien*" (Fries, 1959b). Next to his phanerogamic fascination, he was also strongly interested in mycology and made important contributions to that field. Especially his collections from Bolivia were important because nobody had collected fungi in that part of the continent so far. In retrospect it can be said that his most important scientific work has dealt mainly with Annonaceae and various groups of fungi (Unknown, 1966).

Not only was he active as a botanist but he also held many board positions. During the years 1928-1939, he was vice-secretary of the Academy of Sciences of Sweden; in 1939-1940, he became president of the latter Society and in 1942, he was vice-president. From 1934-1939 he was also president of the Botanical Society of Stockholm, the Dendrological Society (1927-1946), the Linnean Society of Sweden (from 1924-1947; honorary president from 1947 until his death) and the Botanical Society of Sweden (from 1943-unknown; Chardon, 1947).

He was also interested in Swedish botanical history. This could for instance be seen from his presentation at the 7th international botanical congress in Stockholm in 1950 where he presented "A short history of botany in Sweden" (also published in that year). His special interest, however, went to Linnaeus, of which he wrote a biography in 1903 and many other publications after that.

Fries died on January 29, 1966, 90 years old, leaving an extensive and impressive botanical record of accomplishment. During his lifetime he has travelled regularly and collected widely in Sweden, South America, Central Africa, Spain (1906, 1920), and East Africa. Next to his European work, he thus covered two continents with works on taxonomy, phytogeography and mycology. He was righteously called "Sweden's grand old man of botany" (Buchwald, 1970).

TAXONOMIC HISTORY OF THE GENUS *GUATTERIA*

One of Fries' most important contributions to botany has been his (1939) revision of *Guatteria*. Until today, there is still no new revision of this large and taxonomically extremely difficult genus, although a new revision is long overdue. Fries' work can in retrospect easily be criticized but it is an example of good botanical observation, extremely meticulous work, and patience. Fries was able to revise the genus although he had many incomplete collections (i.e. often no flowers or fruits), and had to do without elaborate field work, let alone modern molecular techniques.

The oldest species of *Guatteria* is *Guatteria ouregou*, originally described by Aublet (1775) as *Cananga ouregou*. Nowadays, the generic name *Guatteria* Ruiz et Pav. is conserved. In 1794, *Guatteria* was described by Ruiz and Pavón in their "Prodromus Florae Peruvianae" (Ruiz Lopez & Pavón, 1794) but without any species mentioned. They named their genus after Don Juan Bautista Guátteri, who "died a few months ago, in the bloom of his life". They state that because of his death, the Royal Botanical Gardens of Parma (Italy) now lacked a very distinguished Professor and a very honourable person. In 1798, four new species were included (*Guatteria glauca*, *G. hirsuta*, *G. ovalis* (now *Ruizodendron ovale*), and *G. pendula* (now *Cremastosperma pendulum*; Ruiz Lopez & Pavón, 1798)), without typification of the generic name (the typification method did not yet exist in those days). *Guatteria* was conserved at the Brussels Congress in 1910 and Green typified the name in 1929, designating *G. eriopoda*. However, *G. eriopoda* is not one of Ruiz & Pavón's original species but described only in 1817 (Dunal, 1817). Therefore, in 1993 the type of *Guatteria* was changed to *G. glauca* (after acceptance of a proposal by van Setten & Maas, 1990), this in accordance with the typification of Fries (1959b) and Hutchinson (1923). One disadvantage of the typification on *G. glauca* is that it is a poorly known species. Therefore, the question can be raised if it is the best species to provide the type of the generic name.

Almost twenty years after Ruiz and Pavón's initial description, Dunal (1817) wrote a monograph on the family of Annonaceae in which he mentioned 20 *Guatteria* species. Now is known that his Asian species do not belong to the genus (*Guatteria* is exclusively Neotropical). Dunal described them as such based on the superficially similar monocarps.

Six other species belong to other American Annonaceae genera and only of *G. guianensis* (his *G. aberemoa*), *G. eriopoda, G. glauca, G. hirsuta,* and *G. ouregou* (incl. his *G. podocarpa*) can be said that they rightly belong to the genus. Other early contributions to the taxonomy of *Guatteria* were made by de Saint-Hilaire (1824/25; 5 new species), von Schlechtendahl (1834; 5 new species), von Martius (1841; 20 new species), Triana and Planchon (1862; 11 new species), Diels (1905; 1906; 1924a; 1924b; 1927; 1931; 20 species), and Fries (1938; 12 new species). Because of this work, at the start of Fries' revisionary work in 1939, already 151 species of *Guatteria* had been described. Fries synonymises six of these and transfers 36 species to a different genus. As an addition he places two species in *Guatteria* that had been described into other genera of Annonaceae (*G. axilliflora* (DC.) R.E.Fr. was described as *Annona axilliflora* DC. and *G. guianensis* (Aubl.) R.E.Fr. as *Aberemoa guianensis* Aubl.). He himself then described an enormous amount of 106 new species in his revision (Fries, 1939). These additions made *Guatteria* with 217 species at that time already one of the largest Annonaceae genera. In order to create some order in the taxonomy of *Guatteria* Fries erects 30 sections (table 1; Fries, 1939). Later he recognised two subgenera: *Anomalantha* (containing only *Guatteria anomala*) and *Guatteria* (containing all other species in the genus; Fries, 1955) and several years after that (Fries, 1959b) he reduced the number of sections to 22, merging several not well circumscribed ones (table 1).

Since Fries' treatment the number of species has gradually increased, mainly because of work by Fries himself (Fries, 1947; 1948a; 1948b; 1950; 1952; 1956; 1957a; 1957b; Maguire & al., 1957; Fries, 1959a; Maguire & al., 1960; 36 new species). Next to the occasionally described species, larger recent contributions were made by Maas & al. (1988; 4 new species), Scharf & al. (2005; 2006a; 2006b; 12 new species), and Erkens & al. (this thesis, chapter 9; 5 new species). The total number of species currently recognised approaches 290. For sure, many new species will be described because an enormous amount of unidentified material of *Guatteria* is lying on herbarium shelves around the world, c. 1500 specimens at the Utrecht herbarium alone. However, no doubt exists that a fair amount of recognised species should be put into synonymy. Therefore, current estimates of genus size might be approximately right.

BIOLOGY OF *GUATTERIA* S.L.

Morphologically the genus as a whole is easily recognised by a combination of an impressed primary vein on the upper side of the leaf, valvate sepals, almost always imbricate petals, numerous carpels with a single basal ovule, and a pedicel with a distinct suprabasal articulation (figure 2). However, its species are very homogeneous in many morphological characters, such as habit, flower shape, and monocarp number. Because of a supposed close relationship with *Guatteria,* three smaller genera also constitute a part of Fries' 1939 revision. *Guatteriopsis* (Fries, 1934) is distinguishable from *Guatteria* by the fact that both whorls of petals are valvate (non-overlapping) instead of imbricate (overlapping). *Guatteriella* (Fries, 1939) is characterised by laterally flattened, (hairy) monocarps, thick and densely hairy, brownish yellow petals, and a percurrent straight tertiary venation. *Heteropetalum* (Bentham, 1860) differs from *Guatteria* because the outer petals are greatly reduced in size (becoming almost sepal-like). Together these four genera constitute the so-called *Guatteria* group.

Table 1. Overview of described sections in Guatteria by Fries (1939) and his revisions (1955; 1959b). Monotypic sections *Acrantha* (*G. terminalis*) and *Pycnantha* (*G. elongata*) are described in 1939 but are not mentioned in subsequent publications. Whether Fries submerged or abolished these sections is therefore not clear.

Fries, 1939	**Fries, 1955**	**Fries, 1959**	**Included in**
Section:	**Subgenus:**	**Section (including):**	**this thesis:**
Anomalantha	Anomalantha	---	yes
Acrantha	Guatteria	?	---
Asterantha	Guatteria	---	---
Austroguatteria	Guatteria	Austroguatteria (Asterantha)	yes
Brachystemon	Guatteria	Brachystemon	yes
Cephalocarpus	Guatteria	Cephalocarpus	yes
Chasmantha	Guatteria	Chasmantha	yes
Cordylocarpus	Guatteria	Cordylocarpus	no
Dichrophyllum	Guatteria	Dichrophyllum	yes
Dimorphopetalum	Guatteria	Dimorphopetalum	no
Dolichocarpus	Guatteria	Dolichocarpus	yes
Eu-Guatteria	Guatteria	Guatteria (Macrophyllum)	yes
Leiophyllum	Guatteria	Leiophyllum	yes
Leptophyllum	Guatteria	Leptophyllum	yes
Macroguatteria	Guatteria	Macroguatteria	yes
Macrophyllum	Guatteria	---	---
Mecocarpus	Guatteria	Mecocarpus	yes
Megalophyllum	Guatteria	Megalophyllum	yes
Microcalyx	Guatteria	---	---
Microphyllum	Guatteria	---	---
Oligocarpus	Guatteria	Oligocarpus	yes
Pteropus	Guatteria	Pteropus	yes
Pycnantha	Guatteria	?	---
Sclerophyllum	Guatteria	Sclerophyllum	yes
Stenocarpus	Guatteria	Stenocarpus	yes
Stenophyllum	Guatteria	---	---
Stigmatophyllum	Guatteria	Stigmatophyllum	yes
Trichoclonia	Guatteria	Trichoclonia (Stenophyllum, Microcalyx, Microphyllum)	yes
Trichostemon	Guatteria	Trichostemon	yes
Tylodiscus	Guatteria	Tylodiscus	yes

Species in the *Guatteria* group are mostly small treelets to medium-sized trees that occur in the undergrowth of primary rain forests. Tall trees, such as *Guatteria anomala*, that can grow up to sixty meters, are relatively rare as well as lianas (only two species known, *G. scandens* and an undescribed species from Peru). There are no shrubs but one species is reported to grow as giant bushes (*G. obovata*; Morawetz, 1984). The *Guatteria* group has an exclusively Neotropical distribution (figure 3). The Neotropical region is delimited by the tropics of Cancer and Capricorn, and is part of the Western Hemisphere from 23°27′ North to 23°27′ South latitude. Roughly this is central Mexico to South Brazil (including the northern parts of Argentina and Paraguay; Smith & al., 2004). *Guatteria* can be found throughout this region (except for Argentina and Paraguay) with the most northern species probably being *G. anomala* R.E.Fr. (Mexico) and *G. blainii* (Griseb.) Urb. (Cuba). The most southern occurring species is probably *G. neglecta* R.E.Fr. (Santa Catarina), a probable synonym of *G. australis* A. St.-Hil. Highest species diversity can be found in the Amazon basin, with approximately half of all *Guatteria* species occurring there. The Brazilian coastal areas are also species-rich. Central America harbours some 30 species and the Caribbean Islands only three.

LARGE GENERA

Mega genera (> 500 species; Frodin, 2004) like *Astralagus* (c. 1750 spp.), *Euphorbia* (c. 2000 spp.) or *Carex* (c. 2000 spp.), are a great challenge for taxonomists. Working on such extremely species-rich genera is very exciting but also very problematic. The large size of the genera inhibits comprehensive systematic knowledge and the many nomenclatural changes are challenging. Only few (regional) specialists exist and not much effort is put into the training of young taxonomists to work on these genera (avoidance behaviour). Furthermore, monophyly of the genera and their phylogenetic relationship to other (satellite) genera is not clear. Lastly, especially after molecular phylogenetic analysis there is often a hot debate on whether to "split" or "lump" parts of the genus (Frodin, 2004).

In terms of species-richness, *Guatteria* is much smaller than these mega genera. However, it is one of the largest Neotropical genera that comprises mainly trees, along with *Inga* (Fabaceae, c. 300 species; Richardson & al., 2001a) and *Ocotea* (Lauraceae; c. 300 spp.; Madriñán, 2004; but see Rohwer, 2005). It was therefore clear from the start of the research underlying this thesis, that the above-mentioned problems were relevant to *Guatteria* as well.

Four problems that had to be dealt with were obvious from the start of the project. One of the most important issues in a molecular phylogenetic study is obtaining good quality leaf material that can be used to extract DNA from. Preferably, this material has to be recently collected and dried on silica gel. As mentioned above, *Guatteria* has a wide distributional range and usually does not occur in large populations as many herbaceous plants do. Because time and money were limited, it was impossible to obtain freshly collected leaf material of all or even half the number of *Guatteria* species. However, the c. 4000 herbarium specimens of *Guatteria* present at the Utrecht herbarium provided an invaluable potential resource of DNA.

In order to generate a good phylogenetic hypothesis of species relationships one should sample a sufficient number of species. This is important because it has already been shown

Figure 2. Photo plate illustrating different morphological characters of *Guatteria*. Above: open flower bud (*Guatteria chiriquiensis, Maas 9464*), Below: monocarps and articulation (indicated by an arrow; *Guatteria pudica, Maas 9495*). Photocredit: P.J.M. Maas

that phylogenetic accuracy improves dramatically with the addition of taxa and much more slowly with the addition of characters (Graybeal, 1998). Some systematists use as a rule of thumb that c. 30% of the species in a group should be included in an analysis in order to make any statements about relationships (pers. comm.). For *Guatteria* this meant that at least 85 species should be incorporated. Many widespread species could easily be included, but especially the poorly known and rarely collected species were difficult to collect.

Because of the above-mentioned sampling problems, many herbarium specimens had to be used in this thesis. However, these specimens were never collected for the purpose of DNA based studies, and were therefore often not dried under optimal conditions for DNA conservation. As a consequence, the DNA molecule can be degraded by enzymes and bacteria, fungi, and insects that feed on macromolecules (Eglinton & al., 1991). This degradation in its turn can result in the failure to amplify rather large genome regions (> 500 bp). Degraded DNA requires the use of many more primers and much more lab work in order to obtain sequences of the same quality and length as from freshly collected leaf material. Also population genetic studies using techniques such as AFLP are inhibited when depending on herbarium material that generally yields degraded DNA. Furthermore, some curators opposed to the usage of leaf material of unique herbarium specimens.

The last obvious problem was that of species identification. In general, the species of *Guatteria* show little morphological variation and several species complexes exist. This can result in difficulties when identifying recently collected specimens. Because no recent revision of the genus exists, this problem was partially circumvented in this study. Several type specimens, some of which belong to species complexes, were sequenced in order to determine the closest affinity of unidentified specimens in these complexes. Furthermore, the aim of this study was not to provide a fully resolved species level phylogenetic tree but a framework (the identification of clades) for future work. Therefore, misidentified species pose less of a problem, because the focus is on the monophyletic groups to which they belong.

SPECIES CONCEPTS

The starting point of most phylogenetic studies are taxonomically described species. A complicating factor is that taxonomically recognized species in a clade might not correspond to the evolutionary entities referred to as species (Barraclough & Nee, 2001; Hey, 2001). This is the result of the fact that the concept of "species" can be interpreted in different ways. Nowadays, over twenty species concepts are in use (Mayden, 1997; Hey, 2001), some of them widely others only marginal. Some of these concepts make reference to biological processes (e.g. reproduction and competition) that occur among species (and less so between species) and that contribute to a shared process of evolution within species (Hey, 2001).

The oldest, most widely known and most used species concept is the morphological (or phenetic) concept. This concept defines species as "the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (Cronquist, 1978). This concept uses some particular essential morphological attribute(s) to classify organisms and

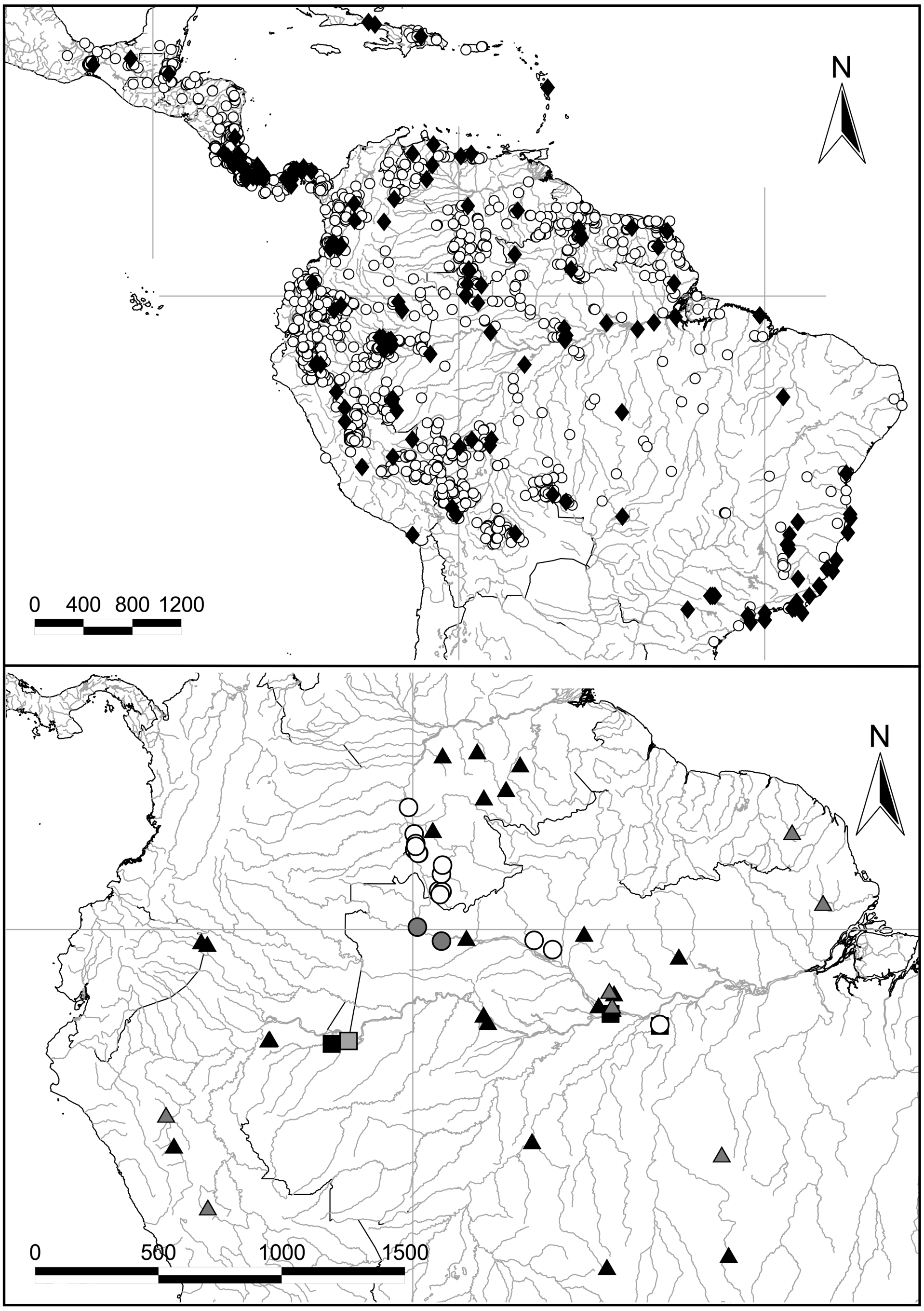


Figure 3. Distribution maps of genera in the *Guatteria* group. Above: *Guatteria*; some localities of specimens (○) and all specimens sampled in this thesis (♦) are indicated. Below: Localities of specimens of *Guatteriopsis* (▲), *Guatteriella* (■) and *Heteropetalum* (○). Localities of specimens sampled in this thesis are indicated with the same symbols but in grey.

is universal (all organisms can be incorporated). It is also easily applicable, making it the most operational concept. The concept makes no reference to biological processes. A disadvantage of this concept is that observed traits of specimens are not evidence for their evolutionary connection (Hull, 1976). Furthermore, the concept is open to intuitive species recognition (Hull, 1997) which is a problem because systematists often do not agree on how to circumscribe a species. There are no objective standards to determine the borders of species, which can make it very difficult to pass on particular species delimitations to future generations.

A second well know species concept is the biological species concept. This concept has been widely used and defines species as "a group of interbreeding natural populations that is reproductively isolated from other such groups" (Mayr & Ashlock, 1991). This concept is thus explicitly built on the concept of reproduction. Although this concept seems to be biologically meaningful, it has a few major drawbacks. Firstly, reproductive isolation is determined at one point in time and from that point onwards two species are defined as separate. Additionally, reproductive isolation usually cannot be tested very easily. Furthermore, the biological species concept is one of the least general concepts because it only applies to sexually reproducing species, asexual organisms cannot be included. This makes the concept pluralistic, because there cannot be one theory for all biodiversity. Several other elements of this concept, such as the lack of lineage perspective, make this appealing sounding concept also less useful from a more theoretical point of view (Mayden & Wood, 1995).

Cladists suppose that the living world is characterized by pattern, and that cladistic methods are the optimal means to discover these patterns (Beatty, 1982). The cladistic species concept is defined as "…that set of organisms between two speciation events, or between one speciation event and one extinction event, or that are descended from a speciation event" (Ridley, 1989). This theory treats species as spatiotemporally restricted entities that form lineages and thus does not refer to biological processes. Furthermore, the nodes in a phylogenetic tree, used in cladistic analyses to determine moments of speciation, are defined on the bases of one or more simultaneous character state changes. Wilkinson (1990; in response to Ridley, 1989), amongst others, has argued against this species concept because speciation as it occurs in nature (for instance by parapatric speciation or polyploidy), contradicts the dichotomous branching process of evolution supposed by cladists (visualised in dichotomous branching trees). This issue is strongly related to the concept of monophyly (see below).

In this study, elements of all three species concepts can be found. For example, specific status is given to the smallest assemblage of individuals (collections) that is morphologically distinguishable from other such assemblages (e.g. this thesis, chapter 9; Chanderbali, 2004). Species so circumscribed possess at least one unifying character or character combination (apomorphy) not found in other species. These apomorphies may be either internally uniform or variable. However, in the case of possible hybridism (e.g. this thesis, chapter 6), a violation of the biological species concept, a previously made distinction between supposed species based on the morphological species concept is questioned. Species concepts should be used in such an iterative approach because the application of these concepts not only depends on their theoretical significance with respect to evolutionary theory but also on their practical applicability and the taxonomic level of analysis. Devising taxa is not an objective process and different researchers will find different taxa. Furthermore, when categorising it should be kept in mind that real evolutionary groups might not be (morphologically or genetically) distinct. In addition, the evolutionary processes that caused the patterns under investigation (and which we use to form taxa) acted long ago (Hey, 2001). Whatever species concept chosen, it should be kept in mind that species circumscriptions are hypotheses, and therefore always subject to change.

PHYLOGENY RECONSTRUCTION: GENERATING PHYLOGENETIC HYPOTHESES

Phylogenetic trees, are the basic structures necessary to think clearly about differences between species, and to analyse those differences statistically (Felsenstein, 2004). In order to produce such a phylogenetic tree (i.e. a phylogenetic hypothesis) from the data at hand (heuristic) tree estimation methods are used. It is impossible to examine all possible trees because the number of (rooted) trees increases rapidly with an increasing number of taxa studied (Felsenstein, 2004). Starting with the assumption that as the time increases since two sequences diverged from their last common ancestor, so does the number of differences between them, tree estimation might be seen as relatively straightforward (Holder & Lewis, 2003). The number of differences between sequences should be calculated and most similar sequences grouped. However, such an approach underestimates the complexity underlying the phylogenetic-inference approach (Holder & Lewis, 2003). In this thesis, two approaches to tree estimation are used in conjunction: the more traditional maximum parsimony method and the relatively new method of Bayesian inference.

The principle of parsimony is a general philosophical principle, introduced by William Ockham (1285-1347; therefore it is also known as "Ockham's razor"). The principle states that when alternative hypotheses explain the data equally well, the simplest one is to be preferred (Sober, 1994). The principle of parsimony is very general and can be applied in the context of methods based on cladistic parsimony, likelihood and Bayesian statistics (de Queiroz & Poe, 2001)

Cladistic methods assume that shared features observed among taxa can be explained by hypotheses of common ancestry that are represented by nested sets of features in hierarchical patterns of taxa (Faith & Cranston, 1991) and were pioneered by Hennig (1950; 1966). The principle of parsimony is used by cladistic methods too choose among phylogenetic hypotheses. This principle should, however, not be confused with the *method* of parsimony (cladistic parsimony; Camin & Sokal, 1965; Farris, 1970; Farris & al., 1970) used in phylogenetic reconstruction (de Queiroz & Poe, 2001). This method for reconstructing an evolutionary tree from discrete character data involves making a reconstruction of changes in a set of characters on a tree and counting the smallest number of times that a character change need have happened (Felsenstein, 1978). The tree (or trees) that includes the fewest character state changes is preferred over all others (Helfenbein & DeSalle, 2005). This method conforms to the general *principle* of parsimony because the amount of hypothesised homoplasies is minimised. The parsimony criterion thus serves to distinguish among alternative patterns with only the simplest assumption about the

relationship between data and pattern (Faith & Cranston, 1991). Little or no background knowledge is required to perform such an analysis and the only assumption underlying this method is the principle of descent with modification (de Queiroz & Poe, 2003).
Cladistic parsimony has two apparent disadvantages. Firstly, in the case of sequence data the "score" of a tree is completely determined by the minimum number of mutations among all reconstructions of ancestral sequences (Holder & Lewis, 2003). However, many plausible scenarios might be able to explain the topology of a tree. Therefore, all possible pathways leading to a certain tree should be investigated because the true phylogeny need not be the shortest one. However, the shortest tree can be used as phylogenetic hypothesis until further evidence indicates otherwise. The second problem is more serious. Parsimony analyses are susceptible to so-called "long branch attraction" (Holder & Lewis, 2003). When this phenomenon occurs, two branches that are not each others sister in the phylogeny, are inferred to be the closest relatives of each other by parsimony.

One of the reasons to justify cladistic parsimony methods is that they minimize ad hoc hypotheses (Faith, 2004). Strictly speaking, cladistic parsimony implies that characters cannot be weighted, consensus methods are not to be used, all data must be combined into a single "total evidence" analysis, and detailed evolutionary models are disallowed (e.g. Kluge, 1998). According to this strict interpretation of cladistic theory, only cladistics itself is satisfactory, and non-cladistic approaches are seen as failing to satisfy basic philosophical requirements (e.g. Kluge, 2002; Faith, 2004). However, any phylogenetic inference method can test statements based on the method's goodness-of-fit values for different tree hypotheses (Faith & Trueman, 2001), and this supposed superiority of cladistic methods is therefore unjustified.

Another reason why cladistic methods might not always be optimal is that genetic data are often the result of complex processes, with many mechanisms that can produce the observed data (Beaumont & Rannala, 2004). For that reason, a Bayesian method is used for comparison in this thesis. The principles of Bayesian statistics date back to Thomas Bayes, a British clergyman and amateur mathematician. In an unpublished manuscript (it was published in 1763, two years after his death) he laid down the principles of his approach for estimating conditional probabilities (Jaynes, 1985). The Bayesian approach was only introduced to phylogenetics in 1996 but quickly gained ground. It builds upon a likelihood foundation and allows complex models of sequence evolution to be implemented (Lewis, 2000; Holder & Lewis, 2003). Furthermore, the primary analysis produces both a tree estimate and measures of uncertainty for the groups on the tree (Holder & Lewis, 2003). It is also possible to incorporate background information into the specification of the model. The most parsimonious hypothesis is the one that maximizes the calculated posterior probability (Beaumont & Rannala, 2004). A drawback of this method is that it can produce excessively high posterior probability values compared to traditional (bootstrap) approaches (Cummings & al., 2003; Simmons & al., 2004).

MONOPHYLETIC VERSUS PARAPHYLETIC GROUPS

There is an extensive debate in literature going on, on the use of monophyletic versus the use of paraphyletic groups in classification (see for instance Dias & al., 2005; Hörandl, 2006 and references therein). Adherents of paraphyly state that dichotomous trees used to visualise phylogenetic relationships are a too strong abstraction and a too simplified visualisation of evolutionary process (Hörandl, 2006). For example, the cladist supposition that species are by definition monophyletic taxa, because ancestral species go extinct after speciation is refuted. This refutation is based on the argument that "parent" species can coexists along with the "daughter" species (e.g. when the speciation process involves budding; Mayr & Bock, 2002), and that therefore paraphyly is acceptable (Wilkinson, 1990; Hörandl, 2006). This difference in approach can be traced back to the fact that the basic assumptions underlying cladistic theory exclude explicit reference to biological processes (see above), while proponents of paraphyletic taxa want to include evolutionary processes into classification (Mayr & Bock, 2002). Because the monophyly/paraphyly discussion is complex, ongoing and well documented in literature, no complete review will be given here.

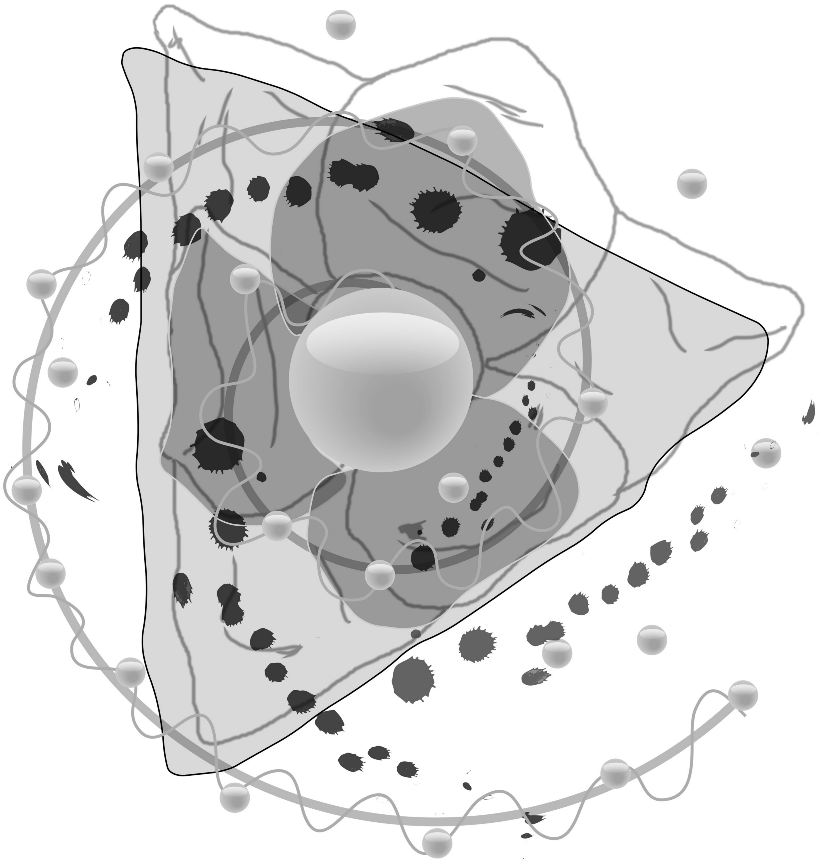
Monophyletic taxa are defined as containing all and only the descendants of some original ancestral group (de Queiroz & Donoghue, 1990). Throughout this thesis, the primary principle of monophyly is used meaning that all recognised taxa should be clades, i.e. monophyletic groups (Hennig, 1966). This because historical groups exist in nature through time (Sanders & Judd, 2000) and only monophyletic taxa can have historical reality (Hennig, 1966). The logical basis for inferring monophyly is that components of a group posses one or more shared, derived character states (synapomorphies). Based on these synapomorphies taxa are combined into one or more hierarchical sets represented by dichotomous branching diagrams (used as a null hypothesis). Secondary principles of monophyly are invoked in order to maximise the stability of a classification, maximise phylogenetic information content, maximise support for monophyly, and maximise the ease of identification (Backlund & Bremer, 1998).

Recognising monophyletic groups is thus a question about the usage of characters. Paraphyletic groups can only be diagnosed on the basis of plesiomorphic (ancestral) characters, i.e. by the lack of derived characters (apomorphies) that diagnose a subtaxon (Sanders & Judd, 2000). It is impossible to characterise paraphyletic groups without invoking a contrast to characters defining a nested monophyletic group. Phylogenetic position is determined by characters, not by the lack of characters, and therefore only monophyletic groups are acceptable. A paraphyletic group does not describe the distribution of any feature whatsoever and, therefore, supplies no prediction that is not available from another more inclusive group (Dias & al., 2005). Furthermore, analysing paraphyletic clades leads to arbitrary results (de Queiroz, 1988).

CONTENTS AND BUILT-UP OF THESIS

This thesis consists of two parts, a "phylogenetics and evolution" part, and a taxonomic part. The phylogenetic part focuses around the four main aims of the *Guatteria* project: (1) to clarify the phylogenetic position of the *Guatteria* group as a whole in the Annonaceae phylogeny, (2) to elucidate the relationships between the genera in the *Guatteria* group, (3) to produce a phylogenetic tree containing at least half the number of species of *Guatteria*, based on multiple sequences of the plastid genome, and (4) to provide insight into the evolution of key morphological and anatomical characters by character mapping onto the phylogenetic tree. The phylogenetic position of the *Guatteria* group is investigated in chapter 2. In chapter 4, a phylogenetic tree of *Guatteria* is used to investigate the diversification patterns in the genus. The relationships between the genera in the *Guatteria* group are explored in chapters 5. Since *Guatteria* is the largest Annonaceae genus, it is sometimes seen as an example of a radiation. To find out if *Guatteria* as a whole indeed constitutes a radiation, the family phylogeny is investigated in chapter 3 with methods that are able to detect radiations. Lastly, one of the numerous species complexes in *Guatteria* is investigated with DNA fingerprinting methods in order to investigate the possible contribution of these methods to the elucidation of taxonomical problems in this complex (chapter 6). As a spin off, the elaborate use of herbarium specimens in this thesis is further investigated with the purpose of improving the selection criteria of vouchers. This can help to maximise DNA extraction and amplification success and decrease destruction of valuable herbarium material (chapter 7). This part of the thesis will be concluded with a discussion (chapter 8) on several topics not covered in the separate chapters.

The systematic part of this thesis focuses around a treatment of the Central American species of *Guatteria* for Flora Mesoamericana (chapter 10). This treatment includes several new species that were discovered during fieldwork in Costa Rica and Panama (chapter 9). Furthermore, as additional data source for fieldwork, a list of vernacular names is included (chapter 11). Vernacular names can be very useful when communicating with non-(professional) botanists (e.g. field guides or locals). The inclusion of this list is meant as an aid for finding *Guatteria* species in the field by asking for the locality of the trees with help of the vernacular instead of scientific name. Lastly, as a guideline into the difficult taxonomy and nomenclature of the genus the most up-to-date list of published names is included as an appendix to this thesis (appendix 2).



2 PHYLOGENETIC RELATIONSHIPS, SATURATION AND MARKER-USE IN THE LONG BRANCH CLADE OF ANNONACEAE

Roy H. J. Erkens, Lars W. Chatrou[2], Jan. W. Maas[1] &
Michael D. Pirie[3]

ABSTRACT

The high level of morphological homoplasy in Annonaceae necessitates the use molecular methods in order to resolve the higher-level relationships in the family. Clarity of phylogenetic relationships is important because a wealth of morphological data are available but the lack of a phylogenetic framework has prohibited evolutionary interpretation of this data. In this study the relationships among the genera of the Long Branch Clade of Annonaceae are elucidated. The only remaining uncertainty revolves around the placement of *Guatteria* and a clade containing the *Duguetia* group and *Xylopia* and *Artabotrys*. Long branch attraction could be causing this result. Furthermore, the plastid *rbcL, matK, ndhF, atpB-rbcL, trnS-G, trnT-L, trnT-F* and *psbA-trnH* regions were investigated with respect to saturation and usefulness in phylogenetic reconstruction. *ndhF* and *trnL-F* prove to provide sufficient data to produce a completely resolved and overall strongly supported topology. *matK* carries little phylogenetic signal and *rbcL* slightly more, for recovering phylogenetic relationships in Annonaceae but both to a far lesser extent than *ndhF*. The non-coding regions *atpB-rbcL, trnS-G* and *psbA-trnH* (the only region showing signs of saturation) seem to contribute most to elucidating relationships at lower taxonomic levels and their use at inter- and infrageneric level should be further explored, as does the sometimes difficult to align *trnT-L* region.

Keywords: molecular phylogenetics, Long Branch Clade, saturation, marker use, long-branch attraction

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INTRODUCTION

The pan-tropical family Annonaceae is the largest family in the order of the Magnoliales (Sauquet & al., 2003) and is found predominantly in tropical lowland rain forests. It comprises around 130 genera and 2500 species of trees and lianas. Thus far, several classifications of the family have been proposed (reviewed in Koek-Noorman & al., 1990), the last comprehensive ones dating back to Fries (1959b) and Hutchinson (1923; 1964). Fries' classification was mainly based on floral characters. He recognised two subfamilies, three tribes and fourteen genus groups. However, analyses of pollen ultrastructure and recent phylogenetic analyses contradict his, as well as other previously proposed classifications. Ever since these classifications were made, much new material has been collected. These new collections call for an update of these outdated classifications. To this moment, no new classification and subdivision of the family has been proposed because phylogenetic relationships within the family have not been fully resolved.

To facilitate a new classification and systematic and evolutionary research on Annonaceae, a phylogenetic tree for the family based on *rbcL* and *trnL-F* sequences was generated (Richardson & al., 2004) consisting of 79 of the c. 130 genera, extending previous molecular work that had more limited sampling and insufficient resolution to elucidate all infrafamiliar relationships (Bygrave, 2000). The genus *Anaxagorea* is sister to the rest of the family (figure 1; Doyle & al., 2000; Sauquet & al., 2003; Richardson & al., 2004). The family is then further subdivided into the 'Ambavioid' clade (sensu Doyle & Le Thomas, 1997a, including genera such as *Ambavia*, *Cananga* and *Tetrameranthus*) and a clade containing the majority of species in the family (figure 1). The latter clade can be further subdivided in the to what have been termed the Long Branch Clade (LBC) and Short Branch Clade (SBC; Richardson & al., 2004). This informal naming reflects the seemingly different rates of molecular evolution between these clades, which has led to significantly different branch lengths from the common ancestors of the two clades to the terminals (Richardson & al., 2004). In addition, in general (bootstrap) supported resolution is higher in the LBC. The crown ages of both clades are approximately the same and estimated to be at least between 50 and 65 my (Richardson & al., 2004).

The LBC and SBC are pan-tropically distributed clades comprising the majority of genera and species in Annonaceae. The LBC and the SBC consist of approximately the same number of genera, but the number of species is different. Within the SBC one can find c. 50 genera comprising some 700 species in total. It harbours genera with both monosulcate and disulcate pollen and is predominantly Asian. The LBC contains c. 50 genera and includes all the larger genera of the family (over 1000 species together: *Guatteria*, 280 species; *Annona* (including *Rollinia*), 200 species; *Xylopia*, 145 species; *Artabotrys*, 100 species; *Goniothalamus*, 120 species; *Duguetia*, 95 species; *Uvaria*, 150 species). The remaining c. 500 species of the LBC are divided in c. 40 genera. Furthermore, the LBC contains a clade that predominantly consists of species with a climbing habit (Uvarioids), a minority habit in the family and all genera with (pseudo-)syncarpous fruits. The LBC as a whole has been recognised before by Doyle & al. (2000) and Doyle & Le Thomas (1996) on the basis of the inaperturate pollen type of many of its constituent taxa. In the study of Richardson & al. (2004) the relationships between the genera within the LBC and SBC were not fully resolved. Therefore, Mols & al. (2004) and Pirie & al. (2006) have further investigated the relationships within the SBC and

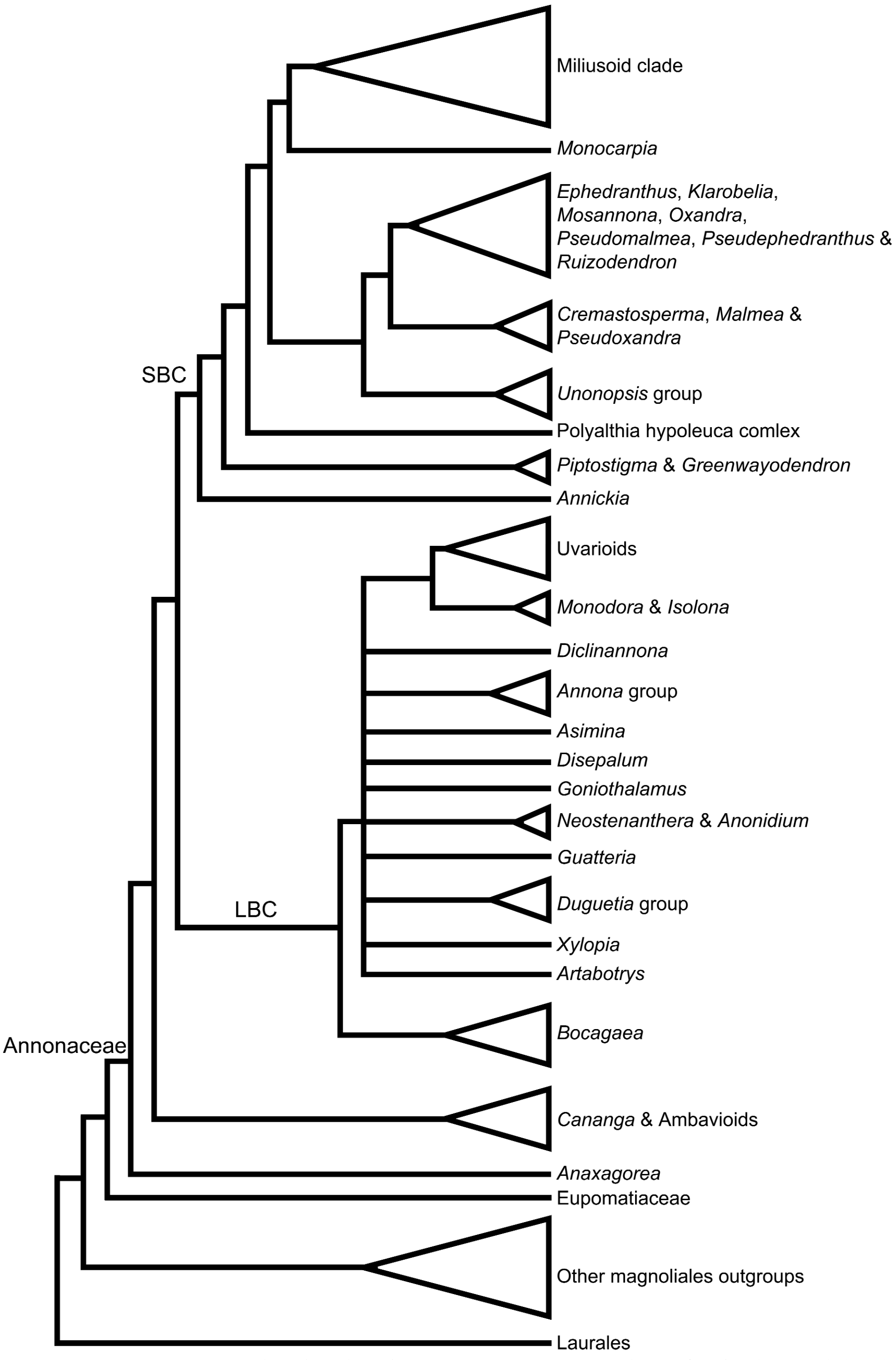


Figure 1. Strict consensus topology based on the maximum parsimony analyses of Richardson & al. (2004) and Pirie & al. (2006). All shown nodes have > 50% bootstrap support. LBC: Long Branch Clade, SBC: Short Branch Clade.

in this study the relationships within the LBC are examined.

Most nodes in the LBC lacked strong bootstrap support (> 90%) on the basis of the *rbcL* and *trnL-F* data (figure 1; Richardson & al., 2004), thereby creating a large internal polytomy. The first unsupported node of importance determines the sistergroup relationships between the unsupported *Xylopia-Artabotrys* clade, the genus *Guatteria* that forms a separate clade, and the weakly supported *Duguetia group* (*Duguetia, Fusaea, Letestudoxa, Pseudartabotrys*). Secondly, the *Annona* clade (including for instance *Goniothalamus, Asimina* and *Disepalum*) is unsupported and its internal relationships are almost completely unresolved.

The high level of morphological homoplasy in Annonaceae makes it necessary to use molecular methods in order to resolve the higher-level relationships in the family (Doyle & Le Thomas, 1996). For instance, *Guatteria* as well as *Artabotrys* have been pointed out as insecurely placed in morphological analyses because in these analyses they caused instabilities (Doyle & Le Thomas, 1996). Clarity of phylogenetic relationships is important because a wealth of morphological data are available and several authors have suggested pathways for the evolution of certain characters. However, evolutionary interpretation of this data has been prohibited because of the lack of a phylogenetic framework.

In this study the available sequence data for the LBC is increased in order to elucidate the relationships among its lineages. Furthermore, the apparent higher amount of molecular evolution in this clade in contrast to the SBC may have lead to saturation in the molecular data, consequently leading to collapsing branches in the phylogeny. This possibility will be investigated using saturation analysis. Lastly, several markers have been used in order to reconstruct phylogenetic relationships in the LBC. Their information content and usefulness for phylogenetic reconstruction is examined.

MATERIALS AND METHODS

Taxon sampling

All clades in the LBC as identified by Richardson & al. (2004) are represented in this study (only the Uvarioids are represented with 3 genera only; voucher specimens in appendix 1). Taxa from the SBC, the Ambavioids and *Anaxagorea* were chosen as outgroups (Richardson & al., 2004).

DNA extraction, amplification and sequencing

Total genomic DNA from fresh silica-dried leaves was extracted using a modified CTAB method (Doyle & Doyle, 1987; this thesis, chapter 7) or the GenElute™ Plant Genomic DNA Miniprep Kit (Sigma-Aldrich Co.). Seven coding and non-coding plastid regions were targeted in this study (figure 2). Previously published *trnL* intron and *trnL-trnF* spacer (*trnL-F*), and *rbcL* sequences were used (Mols & al., 2004; Richardson & al., 2004; Pirie & al., 2005b). To amplify the *matK* region primers 390F, 390F-2 and 1326R (Cuénoud & al., 2002; this thesis, chapter 4) and internal MintF and MintR (Pirie & al., 2005b) were used. For the amplification of the *psbA-trnH* intergenic spacer primers psbA and trnH were utilized (Hamilton, 1999). From the same article the *trnS-G* intergenic spacer primers trnS (GCU) and trnG (UCC) were taken. The *ndh*F gene was amplified with several primer

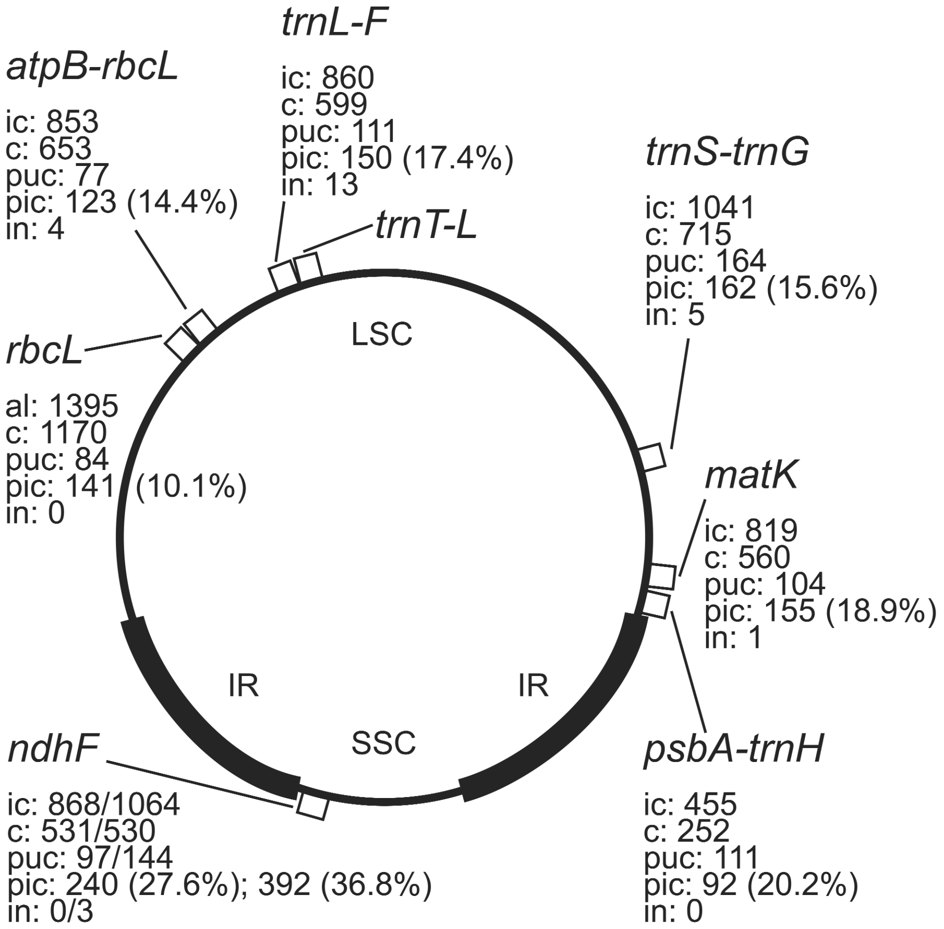


Figure 2. Schematic representation of the location of the *rbcL, matK, ndhF, atpB-rbcL, trnS-G, trnT-L, trnT-F,* and *psbA-trnH* regions on a typical land plant chloroplast genome. The genome is circular and is characterized by two inverted repeat segments (IR) that separate the remainder of the molecule into a large (LSC) and a small (SCR) single copy region. This general structure is found throughout land plants with some exceptions (e.g. conifers and Fabaceae). Several marker statistics are also shown with regard to their performance in the Long Branch Clade of Annonaceae. ic: included characters, c: number of constant characters, puc: number of parsimony uninformative characters, pic: number of parsimony informative characters, in: number of coded indels.

combinations because of its length: 1F, 972F and 2210R (Olmstead & Sweere, 1994), -47F, MF561F, 972R and 1165R (Kim & al., 2001) and Annonaceae specific primers: 689R: 5′-GGCATCRGGYAACCATACATGAAG-3′, LBC-intF: 5′-TCAATAYCTATATGGGGGA AAG-3′, and LBC-intR: 5′-TTCGAAAGGAATTCCTATGRAYCC-3′. The seventh chloroplast region used was the atpB-rbcL intergenic spacer, where the atprbc 3 (complementary to S20 of Hoot & al., 1995) and atprbc2 (Scharaschkin & Doyle, 2005) primers proved sufficient to amplify this region.

In general a standard PCR protocol (35 cycles; 30 sec.: 94°C, 30 sec.: 53°C, 1 min.: 72°C, with an initial 5 min.: 94°C and final 10 min.: 72°C) was used and 0.4% BSA was added to the mixes. For long fragments (> 500 bp) a program with longer cycles and sometimes a lower annealing temperature was applied (28 cycles; 1 min.: 94°C, 1 min.: 50°C or 53°C, 2 min.: 72°C, with an initial 5 min.: 94°C and final 10 min.: 72°C). When necessary PCR products of low concentration were re-amplified in order to obtain sufficient material for sequencing. PCR products were purified using the QIAquick PCR purification kit (Qiagen). For cycle-sequence reactions the same primers were used as for amplifying the particular region, except for the *trnS-G* intergenic spacer. Most lineages appeared to have a poly-A/T run in the *trnG* intron near the 3´*trnG* end. Usually this did not affect the sequence reaction. However, for some taxa it was necessary to apply two new primers to overcome this sequencing problem: trnSint (internal forward): 5′-GTTTGARCRCTTGAGTCC-3′ and trnGint (internal reverse): 5′- CCAAAWTTTATGAATTTKGGTCA-3′. Cycle-sequencing was done with DYE-ET (Amersham) or BIGDYE (ABI) terminators and run on an ABI 3730XL automated DNA sequencer.

Phylogenetic analysis

Sequences were edited and assembled in SeqMan 4.0 (DNAStar Inc., Madison, WI), alignment was done by eye and simple gap coding was applied (Simmons & Ochoterena, 2000). All data partitions were analysed separately but to strengthen phylogenetic signal the combined data partitions were also analysed. Furthermore, analyses were run with different combinations of data partitions to investigate the resolving power of these different combinations. All most-parsimonious trees were generated using PAUP* 4.0b10 (Swofford, 2003) from 10,000 replicates of random taxon addition and swapped using tree bisection-reconnection (TBR), and equal weights. Bootstrap analysis (Felsenstein, 1985) with 10,000 replicates of 25 additional sequence replicates was performed with equal weights and TBR swapping. Bootstrap support of 50–74% is considered to represent weak support, 75–89% moderate support and 90–100% strong support.

Detection of saturation

Saturation analyses (Griffiths, 1997) were conducted to search for saturated data partitions as a result of multiple substitutions at single sites. Pairwise sequence divergence was compared to pairwise transition and pairwise transversion divergences at first, second and third codon positions separately for the *matK*, *rbcL* and *ndhF* genes. Pairwise sequence divergence was also compared to pairwise transition and pairwise transversion divergences for the *trnL-F*, *trnS-G*, *atpB-rbcL* and *psbA-trnH* regions as a whole. For a true saturation curve time would be on the horizontal axis. To avoid the pitfalls associated with molecular dating, saturation plots were drawn using three different estimates of divergence to serve as approximations of time since divergence: (a) absolute number of substitutions; (b) uncorrected pairwise divergence (“p”; Nei, 1987); and (c) two-parameter genetic distance (Kimura, 1980).

RESULTS

Phylogeny

A parsimony analysis of all molecular data combined (7357 aligned characters; 36 coded gaps; 1716 parsimony informative characters) yielded two most parsimonious trees of 5405 steps (figure 3) with a consistency index (CI) of 0.62 and a retention index (RI) of 0.69. The LBC is a strongly supported monophyletic group (bootstrap support (BS) 100%) and the Bocageeae are sister to all other species within the LBC (BS 100%). The LBC without the

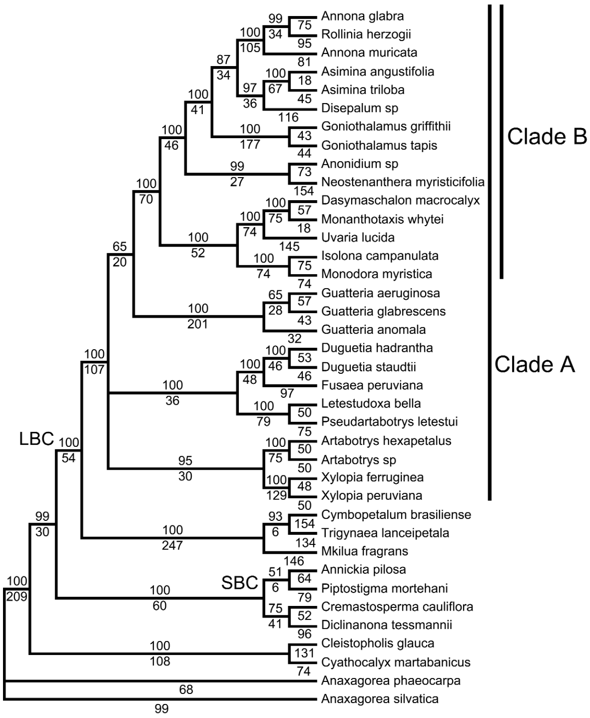


Figure 3. One out of two most parsimonious trees, based on *rbcL, matK, ndhF, atpB-rbcL, trnS-G, trnT-F,* and *psbA-trnH* sequence data. Branch lengths are indicated below the branches, bootstrap support values above. LBC: Long Branch Clade; SBC: Short Branch Clade.

Bocageeae will from hereon be referred to as Clade A (figure 3). Overall the topology of Clade A is strongly supported. One exception is the relationship between the *Duguetia group*, the *Xylopia-Artabotrys*-clade and the remainder of the genera. These three lineages form an internal polytomy. Also, there is weak support for the position of *Guatteria* as sister to the remaining genera of the LBC (BS 65%), a clade that will be referred to as clade B (figure 3). Finally, the sistergroup relationship between *Annona* (including *Rollinia*) and the *Asimina-Disepalum*-clade is only moderately supported (BS 87%). The position of *Diclinanona tessmannii* is surprising. This species is placed strongly supported within the SBC (BS 100%), an outgroup in this study. Analyses of the separate plastid regions resulted in most parsimonious trees that were congruent but always less resolved than the most parsimonious trees from the combined analysis (data not shown). Phylogenetic analysis of the *ndhF* region in combination with the *trnL-F* region was sufficient to produce a completely resolved and overall better supported tree than the trees from the total evidence analysis (figure 4; 2970 steps long, CI 0.58; RI 0.67; compare to figure 3). All nodes receive strong bootstrap support except two. The node subtending the *Duguetia group* and the *Xylopia-Artabotrys*-clade is only weakly supported (BS 67%), as is the sistergroup relationship of this clade with Clade B (BS 51%). The position of *Guatteria* is different from that in the tree based on all data partitions. In the *ndhF/trnL-F* analysis the genus is sister to all genera of Clade A (figure 4).

Saturation analysis

Saturation analyses using three different types of genetic distance measure (absolute number of substitutions, uncorrected pairwise divergence and two-parameter genetic distance) yielded the same result. Therefore, only the uncorrected pairwise divergence ("p") plots are discussed and shown here, since this divergence measure is the most commonly used.

Saturation plots for the *rbcL, matK, ndhF, atpB-rbcL, trnS-G, trnT-F* and *psbA-trnH* regions (figure 5) show that the slope of transversions (G↔T; C↔A) always lies below that of transitions (A↔G; C↔T). This indicates that transversions occur less frequently than

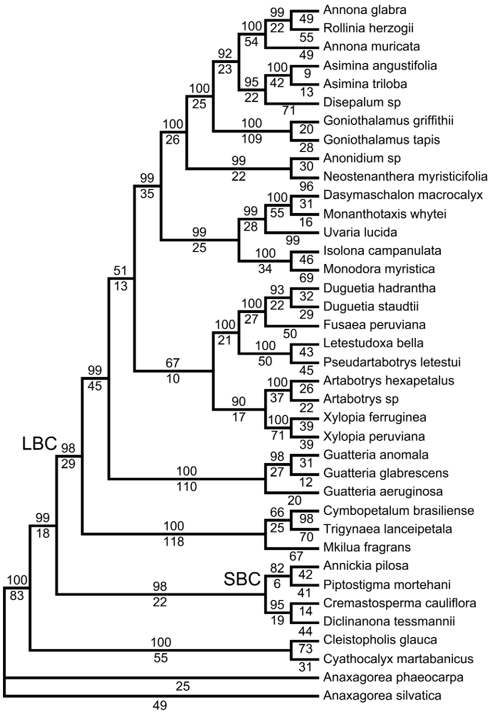


Figure 4. The single most parsimonious tree, based on *ndhF* and *trnT-F* sequence data. Branch lengths are indicated below the branches, bootstrap support values above. LBC: Long Branch Clade; SBC: Short Branch Clade.

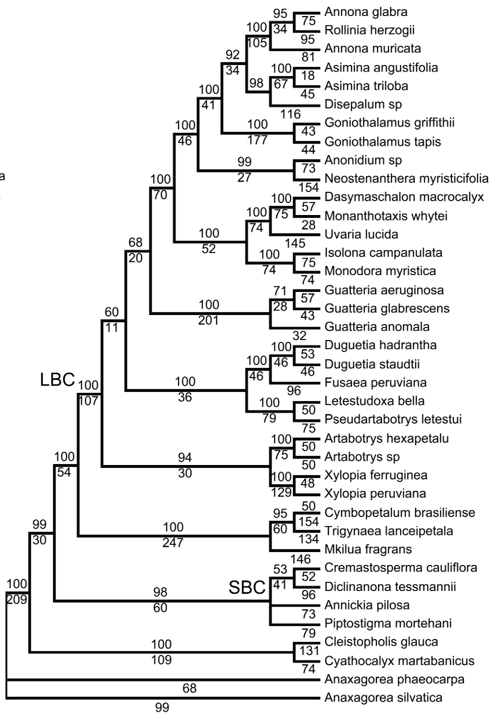


Figure 6. The single most parsimonious tree, based on *rbcL, matK, ndhF, atpB-rbcL, trnS-G, trnT-F,* and *psbA-trnH* sequence data, after down-weighting transitions in *psbA-trnH*. Branch lengths are indicated below the branches, bootstrap support values above.

transitions. None of the plots of the different data partitions show clear levelling off associated with saturation except for the transitions in the *psbA-trnH* region. Here levelling off occurs at 15-20% uncorrected sequence divergence (figure 5). To take into account this apparent saturation a step-matrix was constructed in PAUP to down-weight transitions over transversions by a factor of 2 to 1. The weighted parsimony analysis resulted in one tree of 5682 steps (figure 6; CI 0.61; RI 0.68). The tree is completely congruent with that of the unweighted analysis (figure 3). Most nodes are now strongly supported. Only the sistergroup relationship of the *Duguetia* group to *Guatteria* and Clade B, and the sistergroup relationship of *Guatteria* to Clade B receive weak support (BS 60% and BS 68% respectively). The topology differs from that solely based on the *ndhF* and *trnL-F* regions (figure 4) with respect to the position of the *Guatteria* group, the *Duguetia* group and the *Xylopia-Artabotrys*-clade

For the saturation analyses, the *matK*, *rbcL* and *ndhF* regions were also analysed per codon position (figure 7). Again, all plots show that the slope of transversions lie below that of transitions, showing more constraints on the occurrence of transversions than on transitions. Furthermore, the plots show that differences in rate of evolution per codon position are in general as expected. In terms of encoding a specific amino acid, the first

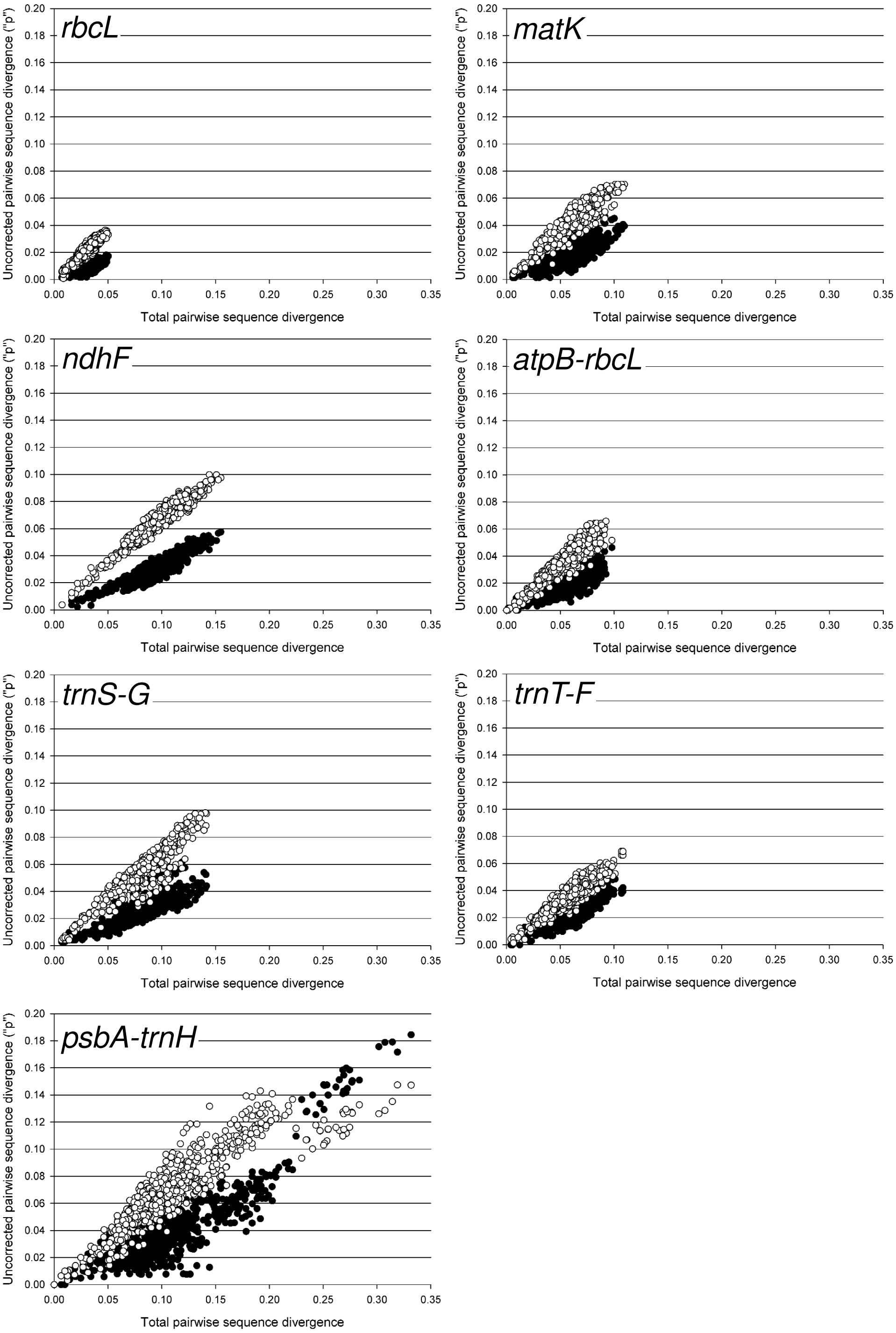


Figure 5. Uncorrected pairwise sequence divergence (”p”) for transitions (○) and transversions (●) plotted against the total amount of pairwise sequence divergence (”p”).

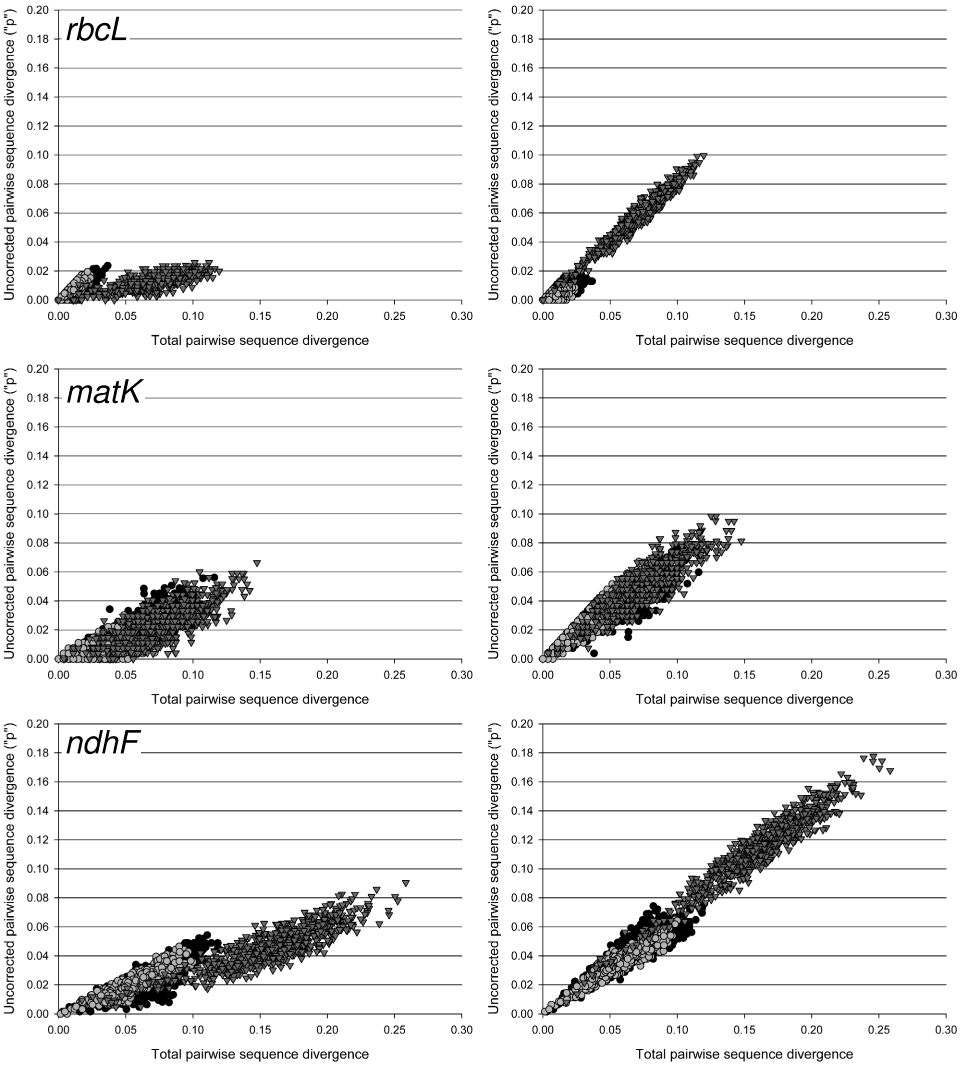


Figure 7. Uncorrected pairwise sequence divergence (”p”) for first (●), second (○) and third (▽) codon position plotted against the total amount of pairwise sequence divergence (”p”) for the *rbcL, matK* and *ndhF* region. Transversions (left) as well as transitions (right) are shown.

codon position is more functionally constrained than the third codon position but less functionally constrained than the second codon position, on average (figure 7). *ndhF* behaves near clocklike with respect to both transitions and transversions (i.e. an increase in the number of transitions or transversion is proportional to an increase in total sequence divergence). Because the *ndhF* region consists of two parts with different characteristics (see below), both parts were also analysed separately (figure 8). Also analysed in this way, both regions exhibit near clocklike behaviour. *rbcL* shows a pattern similar to *ndhF* (figure 7). With regard to *matK*, all codon positions and transversions as well as transitions show considerable amount of variation, indicating no clocklike relationship between the amount of sequence divergence and the amount of transitions or transversions.

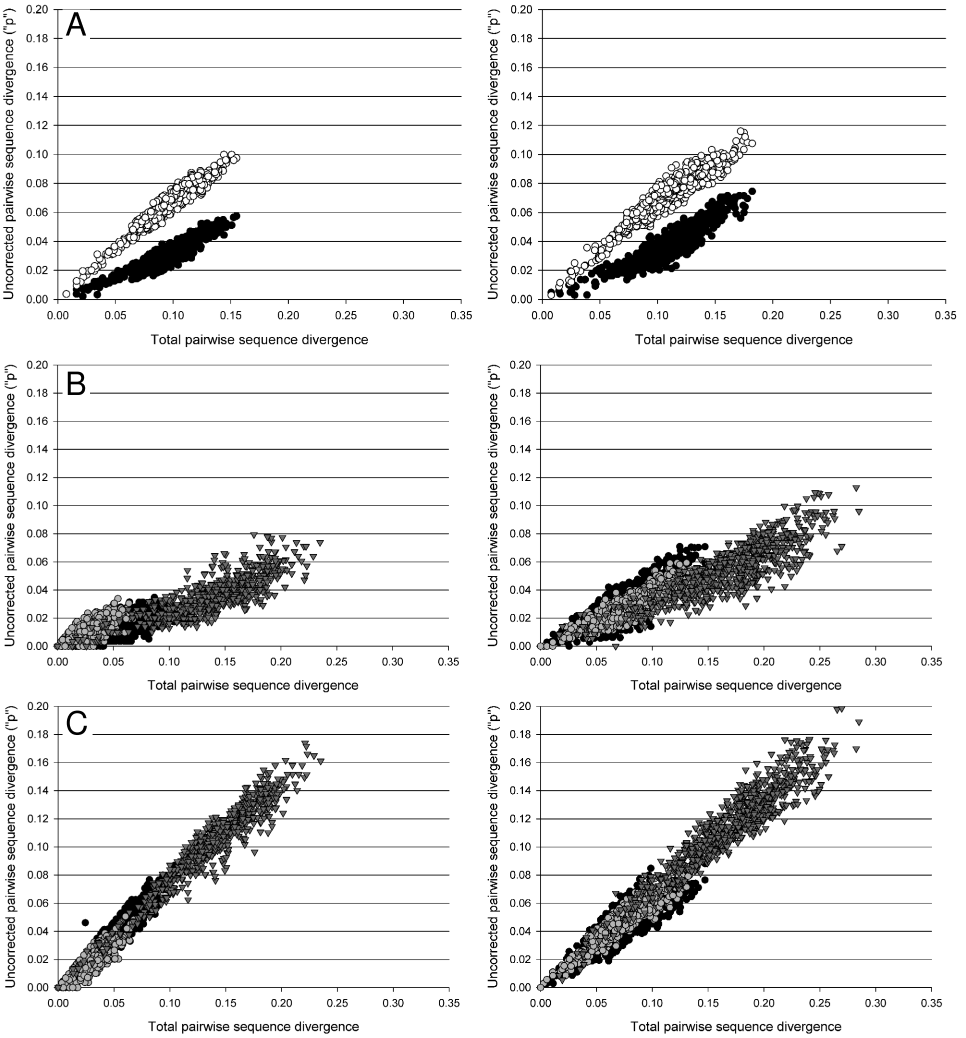


Figure 8. A. Uncorrected pairwise sequence divergence ("p") for transitions (**O**) and transversions (●) plotted against the total amount of pairwise sequence divergence ("p") for the 5′ (left) and 3′ (right) region of *ndhF*. B. Uncorrected pairwise sequence divergence ("p") for first (●), second (**O**) and third (▽) codon position transversions, and C. transitions plotted against the total amount of pairwise sequence divergence ("p") for the 5′ (left) and 3′ region of *ndhF*.

DISCUSSION

Phylogenetic relationships in the Long Branch Clade

The tree presented in figure 3 confirms the unsupported topology found by Richardson & al. (2004) and further elucidates the relationships among the clades in the Long Branch Clade (LBC) of Annonaceae. Most internal polytomies that were found in that analysis (figure 1) were resolved by roughly tripling the amount of sequence data. The only polytomy that remains contains three lineages: the *Duguetia group*, the *Xylopia-Artabotrys*-clade and the remainder of the species of the LBC (figure 3). Such a polytomy can be caused by insufficient synapomorphies, conflict in the supporting characters (homoplasy) or multiple substitutions. It seems that a lack of characters is not the main reason for a lack of support in this part of the topology. Although the unsupported branches are seemingly shorter (with only 11 and 36 substitutions), they are not significantly so (average LBC: 79.0, stdev: 57.4).

Conflict in supporting characters may also contribute to the lack of support in figure 3. The two trees at the basis of the strict consensus of figure 3 differ with regard to the position of the *Duguetia* group and the *Xylopia-Artabotrys*-clade (data not shown). In the first tree these clades are sister to each other (and together sister to *Guatteria* and Clade B), in the second tree their relationship is as in figure 4.

A third factor responsible for a lack of support might be saturation. It is known that mutation rates can vary substantially among sites and that certain sites appear to change at remarkably high rates. This can lead to phylogenetically informative characters that are saturated with multiple hits. Homoplasy is significantly higher for such characters and resolution of the phylogenetic hypothesis is significantly improved by removal of these saturated characters. Saturation analysis were carried out to identify partitions in the data that might contribute a large degree of noise instead of signal to phylogenetic reconstruction. It was found that only *psbA-trnH* showed signs of saturation (figure 5, 7 and 8) and after down-weighting these saturated characters, the resulting topology was completely resolved (with the exception of relationships in the SBC outgroup) and overall strongly supported (figure 6). This suggests that the lack of resolution and lower nodal support for some nodes were at least partially attributable to saturation.

The different placements of the *Guatteria* clade, the *Duguetia group* and the *Xylopia-Artabotrys*-clade are in all analyses only weakly supported (figure 3, 4 and 6). This means that the phylogenetic position of these clades should be regarded as ambiguous. Interestingly, *Guatteria* was also insecurely placed in morphological analyses (Doyle & Le Thomas, 1996). It seems that neither molecules nor morphology are thus far able to provide definitive insight in the phylogenetic position of this genus. With regard to molecules, this phylogenetic uncertainty might be the result of the fact that taxa with particularly long subtending branches can be grouped with other such taxa because parallelisms and reversals are misinterpreted as evidence for a shared phylogenetic history (Felsenstein, 1978; Steel, 1993) This so called long-branch attraction might influence the reconstruction of relationships in the LBC because of the long branch subtending the *Guatteria* clade. This branch is the second longest in the LBC. If taxa can be added to break it up, it is much more preferable to add these taxa than to add more characters (Graybeal, 1998) because adding more sequence data results in stronger evidence for the incorrect topology (Soltis & al., 2004).

Only 21 out of c. 50 genera in the LBC were used in this analysis. The Uvarioids are only represented with three genera instead of the seven genera used by Richardson & al. (2004). However, this clade is already strongly supported (BS 100%) in Richardson's & al. analysis and the unsampled taxa are therefore believed to be monophyletic with the three genera included here. Next to this, due to the unavailability of recently collected, silica-dried material of African taxa these are mainly missing from this study. To investigate the effect of their exclusion, preliminary analyses of incomplete sequence data of 11 non-included small (African) genera have been carried out (e.g. *Uvariastrum, Meiocarpidium, Mischogyne*).

These revealed no major topological changes (Couvreur, pers. comm.), since the added genera clustered within already identified clades in the LBC (e.g. with *Isolona* and *Monodora*). Therefore, probably no taxa exist that could break up the long branch subtending *Guatteria*.

Most of the previously found polytomies in the LBC (Richardson & al., 2004) should be regarded as uncertainty of phylogenetic relationships ("soft polytomy"; Maddison, 1989) that could be resolved by adding more sequence data and downweighting saturated characters (i.e. they were an analytical artefact). These polytomies did not represent the actual simultaneous origin of different lineages ("hard polytomy"). The latter polytomy cannot (easily) be resolved because it is the result of the biological history of the group. It has been shown that utilizing the same amount of sequence data as was done in this study, also lead to an increased resolution for a part of the SBC (Pirie & al., 2006), although several nodes were still weakly supported. Adding more data might also be tried to resolve the relationships in the Miliusoid clade, something that could not be done on the bases of *rbcL*, *matK* and *trnL-F* alone (Mols & al., 2004). However, given the difference in supporting characters between the LBC and the SBC on the basis of equal data sets, it might be true that the factors responsible for the many polytomies in the SBC (and especially the Miliusoid clade) might be different from those in the LBC.

Diclinanona tessmannii has a completely different placement when compared to previous analyses (Richardson & al., 2004). It proves to belong to the SBC instead of the LBC. *Diclinanona* was previously placed in an unsupported clade together with a.o. *Goniothalamus* and *Annona*. Due to conflict in placement of *Diclinanona* on the basis of newly generated plastid sequences and previously published *trnL-F* and *rbcL* sequences, the latter regions were re-amplified and sequenced. This resulted in *trnL-F* and *rbcL* sequences that confirmed *Diclinanona*'s new position on the basis of the other plastid regions.

Marker utility

In this study several markers from different regions of the chloroplast were used. With the exception of *psbA-trnH* none of these markers showed signs of saturation (figure 5). Although not saturated, *matK* seems to be least constrained in terms of mutation rate at all codon positions (figure 7). When these results are linked to for instance their phylogenetic information content, this can help us to understanding the usefulness of these markers in Annonaceae research.

Three coding regions have been used in this study. The *rbcL* region contained the least amount of parsimony informative characters (PIC; 10.1%; figure 2). *rbcL* was one of the first markers used on a larger scale in phylogenetic systematics. It has been sequenced for over 5000 species (Sanderson & Driskell, 2003) and has been used in one of the largest single phylogenetic studies ever done (Källersjö & al., 1998). The *rbcL* gene is located in the large single copy region of the chloroplast genome (figure 2) and encodes the large subunit of ribulose 1,5-biphosphate carboxylase/oxygenase (RUBISCO; a critical photosynthetic enzyme; Soltis & Soltis, 1998). It is still first choice to infer relationships at family level and above, but the lower limit of its applicability is genus (or sometimes species) level. It has been shown that sequencing past the *rbcL* stop codon up to the 3′ amplification primer can provide extra parsimony-informative sites (e.g. Soltis & al., 1996; Mols & al., 2004). Because saturation does not pose a problem for this gene region (figure 5 and 7), it seems suitable for phylogeny reconstruction in Annonaceae. However, separate phylogenetic analysis of this region resulted a consensus tree that was only partially resolved (data not shown). This might indicate that *rbcL* is less suitable for elucidating intergeneric relationships in Annonaceae, although it could contribute to the separation of larger clades.

The *matK* region contained 18.1% PIC. *matK* encodes a protein (maturase) involved in splicing type II introns from RNA transcripts (Neuhaus & Link, 1987; Wolfe & al., 1992) and is located in the large single-copy region of the chloroplast genome (figure 2; Soltis & Soltis, 1998). The region is easily amplified due to highly conserved coding regions or the use of internal primers. It is said to be one of the most rapidly evolving plastid genes (Wolfe, 1991). This pattern can be confirmed here, *matK* does not only contain almost twice as much PIC as *rbcL* does, but saturation analyses show that it is least constrained with regard to mutation at all codon positions (figure 7). Indeed, it has been found that substitution rates in *matK* codon positions are not as strongly skewed towards third position as normally is the case in genes like *rbcL* (Müller & al., 2006). It has been suggested that the large number of variable sites in *matK* make the gene appropriate for resolving intergeneric and even interspecific relationships but resolutions were often unsatisfactory (Sang, 2002). Here, separate phylogenetic analysis of this region resulted in a completely collapsed consensus tree (data not shown). Surprisingly, partial *matK* sequences were able to produce a phylogenetic tree of Angiosperms (Hilu & al., 2003) that was comparable in resolution and support to trees inferred from *rbcL*, *atpB* and 18S (Soltis & al., 2000). The application of this relatively rapid evolving region at the level of major flowering plant lineages was surprising because of the expected effect of multiple hits and thus high levels of homoplasy and saturation (Müller & al., 2006). The effort of amplifying this marker for phylogenetic work in Annonaceae could be questioned in the light of the results presented here and those of other studies.

The region that contained most PIC (29.6%) and in itself produced a single completely resolved topology was *ndhF* (data not shown), congruent with that of figure 4 (although in the separate analysis the position of *Guatteria* and the clade containing the *Duguetia* group together with the *Xylopia-Artabotrys* clade was not bootstrap supported). In contrast to *rbcL* and *matK*, the protein coding *ndhF* gene is located in the small single-copy region of the chloroplast genome, close to the junction of the inverted repeat (figure 2; Soltis & Soltis, 1998). It encodes a subunit of chloroplast NADH dehydrogenase (Olmstead & Reeves, 1995) and consist of two regions. The 5′ region of the gene has been reported to be more similar to *rbcL* in both rate and pattern of nucleotide substitution, the 3′ part is reported as more A/T rich, with higher levels of nonsynonymous base substitution and a transversions bias at all codon positions (Kim & Jansen, 1995). Here it is found that both regions exhibit higher nucleotide substitution rates for all positions when compared to *rbcL* and *matK* (figure 7 and 8). The total pairwise sequence divergence for transitions as well as transversion is higher for the 3′ region than the 5′ region, although the mutation rate (slope) is approximately the same (figure 8). The difference between the 5′ and 3′ region with regard to PIC and the near clocklike behaviour of both parts contributes to the successful utility of this marker in Annonaceae (and other) research. The more conserved 5′ region is useful for inferring relationships in older groups and the more variable 3′ region for use in more recently evolved groups. It has for instance been shown that trees based on *ndhF* are more fully resolved than on the basis of either *rbcL* or *matK* alone (Soltis & Soltis, 1998).

Next to three coding regions, four non-coding regions were drawn upon. The least variable was the *atpB-rbcL* intergenic region (14.4% PIC). This region is located between the 3′ ends of *atpB* and *rbcL* (figure 2) and has been reported to be useful for resolving relationships within and between genera. Another intergenic region is the spacer between *trnS* and *trnG* (*trnS-trnG*; figure 2). This region also has been shown to be highly variable but with 15.6% parsimony informative characters it performs comparable to *atpB-rbcL*. When both regions are analysed separately, *atpB-rbcL* as well as *trnS-trnG* perform only slightly better than *matK*. The backbone of the strict consensus tree is almost unresolved and only several terminal clades are recovered (data not shown).

The *trnL-F* region (*trnL* intron and *trnL-F* spacer) is together with *rbcL* one of the most widely used chloroplast regions in plant systematics (Shaw & al., 2005) and has been used in Annonaceae research before (e.g. Mols & al., 2004; Richardson & al., 2004; Pirie & al., 2006). Its successful employment is mainly due to the near-universal nature of the primers. The region is located in the large single-copy region of the chloroplast (figure 2) and consists of three tandemly arranged transfer RNA genes (*trnT*$_{UGU}$, *trnL*$_{UAA}$ and *trnF*$_{GAA}$) separated by non-coding spacer regions. It has been shown that for Annonaceae a paralogous *trnL-F* copy exists (Pirie & al., 2005a). The region contains 17.4% PIC and when analysed separately produces a tree comparable to the tree recovered by Richardson & al. (2004), thus showing an internal polytomy but recovering most major clades (data not shown).

The *trnT-trnL* region is directly connected to the 3′ of the *trnL-F* region but is not as often used. This spacer provides greater variation than the *trnL-F* region but due to the poorly performing *trnT* primer it is often difficult to amplify. A primer designed by Cronn & al. (2002) can be used to alleviate this problem. Indeed, this primer enabled successful amplification of the *trnT-trnL* region in Annonaceae (e.g. this thesis, chapter 4). Next to amplification problems, the *trnT-trnL* region exhibits a wide range of sizes between genera (e.g. c. 450 bp in *Anaxagorea phaeocarpa* to c. 1600 bp in *Xylopia peruviana*) and includes many large A/T rich regions (also reported for other plant groups; Shaw & al., 2005). Homology assessment was therefore problematic between the sequences of the genera in the LBC and this region could therefore not be used in the analyses done for this study. However, the region can contain many PIC and might be used at infrageneric level since at that level length variation is less and alignment is more straightforward (e.g. this thesis, chapter 4). This marker might therefore contribute substantially to species-level phylogenetic work in Annonaceae.

The most variable but also shortest non-coding region in this study was the *psbA-trnH* spacer region (20.2% PIC; figure 2). The ends of the spacer are relatively conserved compared to the middle portion of the spacer, which is highly indel prone (Aldrich & al., 1988) and proves sometimes difficult to align. The middle region may generate a relatively high amount of homoplasy due to apparent indel "hot spots", with numerous repeating and overlapping indels (Shaw & al., 2005). As has been shown here, *psbA-trnH* showed

signs of saturation, thus confirming these earlier reported results. Separate phylogenetic analysis yielded a mostly collapsing tree with only several terminal groups successfully recovered (data not shown).
From several accessions of *Guatteria* a second, 60 bp shorter and much more invariable copy of *psbA-trnH* could be sequenced. Both ends of this copy (c. 200 bp at the 5′ end and c. 70 at the 3′ end) could be aligned with the "true" *psbA-trnH* but the middle part contained several deletions similar in all accessions. Phylogenetic analysis of this copy together with "true" *psbA-trnH* sequences resulted in erroneous placement of the accessions with the paralogous copy in the outgroup (data not shown). As mentioned above for the *trnL-F* region, the existence of a paralogous copy of a plastid region in Annonaceae has already been shown (Pirie & al., 2005a) and this might be the second incidence of such a copy.

Analysis of the *ndhF* and *trnL-F* plastid regions is sufficient to produce an equally well resolved topology as the one obtained on the basis of all markers used here (figure 3 and 4). This is an important issue because for many studies the choice has to be made between sampling a large number of nucleotides or invest in a denser taxon sampling. Finding genomic regions that provide sufficient signal without compromising taxon representation is therefore essential for accurate assessment of evolutionary histories (Soltis & al., 2004). Nowadays, this is ever more important given the limited funding available for many projects. Because sequencing becomes ever more rapid and inexpensive there is a trend towards uncritically generating as much genomic data as possible. However, taxon sampling is crucial and should not be ignored. Especially when a species level phylogeny for Annonaceae (containing > 2000 species) is aimed at, it is critical to be as cost (and time) effective as possible in generation of sequences. A data matrix based on the *ndhF* and *trnLF* regions might best optimize time and money against phylogenetic accuracy in Annonaceae.

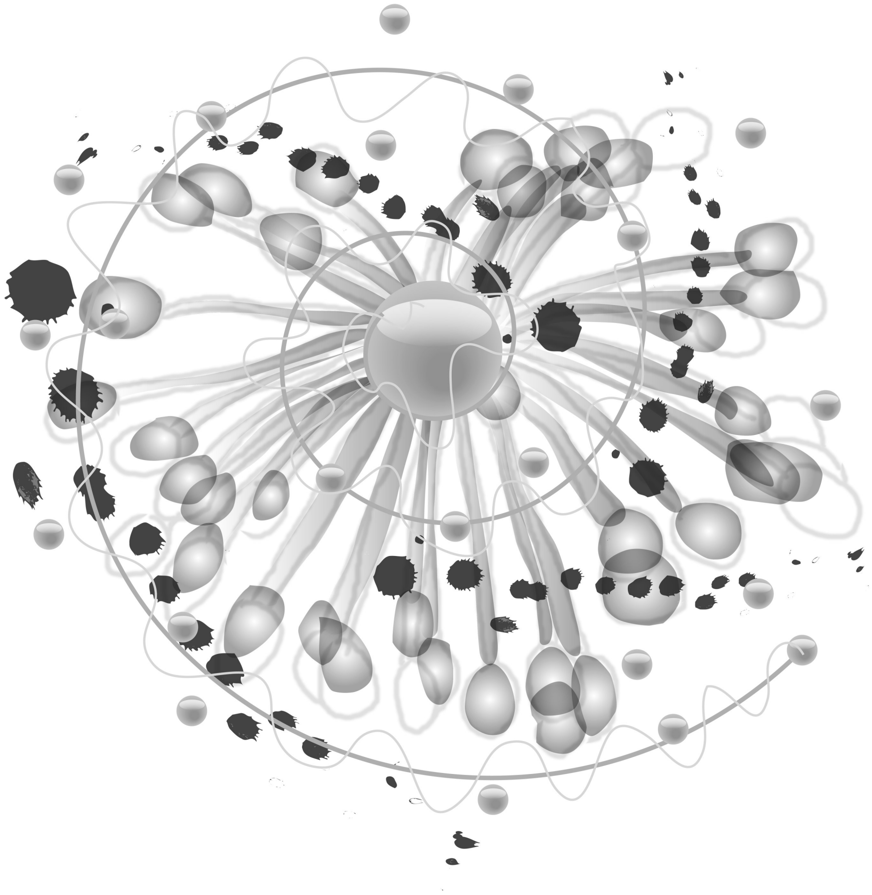
No single plastid marker so far has the power to resolve relationships within the LBC of Annonaceae as well as *ndhF* does. Unfortunately, the gene tree of *ndhF* conflicts with the tree obtained from a total evidence approach based on all plastid regions. In order to differentiate between the different trees another independent data source, such as a (low-copy) nuclear gene, would be useful. Low-copy nuclear genes in plants hold a great potential to improve the robustness of phylogenetic reconstruction, especially at low taxonomic levels where universal plastid DNA markers are unable to generate strong phylogenetic hypotheses (Sang, 2002). Several attempts have been made to use the nuclear ITS, *PHYC* and *ncpGS* regions in Annonaceae. All three markers have proven to be difficult to amplify or homology of the obtained sequences could not unambiguously be established. So far they are not applicable at higher taxonomic levels (i.e. in order to resolve relationships between genera), but *ncpGS* might be useful at species level (e.g. this thesis, chapter 6). A nuclear marker as addition to all already available chloroplast markers is highly desirable, especially in order to elucidate the relationships within the poorly resolved Short Branch Clade (Mols & al., 2004; Pirie & al., 2006).

CONCLUSIONS

The tripling of the amount of sequence data, and dowweighting of saturated characters for the Long Branch Clade of Annonaceae resulted in a completely resolved and overall strongly supported phylogenetic tree. The only remaining uncertainty revolves around the position of *Guatteria* and a clade containing the *Duguetia* group and *Xylopia* and *Artabotrys*. This uncertainty is reflected by the absence of bootstrap support for the nodes in question. It is therefore best to regard these relationships as unresolved. The ambiguous placement might be the result of long branch attraction resulting from the long branch subtending *Guatteria*.

The plastid *rbcL, matK, ndhF, atpB-rbcL, trnS-G, trnT-L, trnT-F* and *psbA-trnH* regions were investigated with respect to saturation and usefulness in phylogenetic reconstruction. With the exception of *psbA-trnH*, no markers showed signs of saturation. The combination of *ndhF* and *trnL-F* seems sufficient to produce an equally well supported tree in comparison with all data used. Of the coding regions, *matK* seems to contribute little to recovering phylogenetic relationships in Annonaceae and its further use should be questioned. *rbcL* does contribute to the recovery of phylogenetic relationships but to a far lesser extent than *ndhF*. *atpB-rbcL, trnS-G* and *psbA-trnH* seem to contribute most to elucidating relationships at lower taxonomic levels and their use at that level should be further explored, as goes for the sometimes difficult to align *trnT-L* region. A low-copy nuclear marker that is straightforward to use is still lacking in Annonaceae although the use of several (e.g. ITS, *PHYC* and *ncpGS*) has been explored.

The results of this study are in concordance with previously obtained phylogenetic data (Mols, 2004; Richardson & al., 2004; Pirie & al., 2006). Together they give a sound basis for the construction of a phylogeny of the family of Annonaceae as a whole. This phylogenetic hypothesis will then facilitate future re-interpretation of all available morphological data and postulated evolutionary pathways. This in its turn contributes to our understanding of the evolution of the largest family in the order of the Magnoliales.



3 DIVERSIFICATION RATE-SHIFT PATTERNS IN ANNONACEAE, PINPOINTING THE RADIATIONS

Roy H. J. Erkens & Lars W. Chatrou[1]

ABSTRACT

Biologists are fascinated by species-rich groups and would like to discover the causes for abundant diversification. Understanding the evolution of the family of Annonaceae (c. 2500 species in 130 genera) can contribute greatly to our understanding of the processes that have led to the assembly of current day biodiversity. The available phylogenetic data on Annonaceae and dates for all the clades in the family can be used to study diversification patterns in order to identify factors that drive speciation and the evolution of morphological (key-) characters. In this study it was found that, except for *Goniothalamus*, the largest genera in the family are not the result of radiations. Furthermore, the difference in species numbers between the Long Branch Clade and Short Branch Clade cannot be attributed to significant differences in diversification rate. Most of the speciation within Annonaceae is not discernible from a stochastic ERM branching model (i.e. chance) and no special explanations are therefore necessary for the distribution of species-richness across the major part of the Annonaceae phylogeny. Because of geographic structure, a number of clades might be species-rich as the result of a radiation after a founder event. Also, large clade sizes within Annonaceae need not have resulted from intrinsic key-innovations that have influenced the rate of diversification. Only for a small number of clades, key-innovations might be invoked to explain the elevated rate of diversification.

Keywords: supertree analysis, temporal method, topological method, key-innovations, stochastic branching pattern

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INTRODUCTION

Biologists are fascinated by species-rich groups because their size is associated with evolutionary success (Raikow, 1988). Researchers would like to discover the causes for abundant diversification in order to understand the processes that have led to the assembly of current day biodiversity. Therefore, studying the evolution of large clades is a major theme in systematic research these days. The family of Annonaceae is a pan-tropical family, placed within the order of the Magnoliales (APG-II, 2003). The family can be found predominantly in low-land tropical rain forests and comprises some 2500 species in 130 genera (Chatrou & al., 2004). Because of its abundance, understanding the evolution of this large family can contribute greatly to our understanding of the factors responsible for the maintenance of biodiversity.

Species-rich groups are often thought to be the result of a radiation. Indeed, studies that invoke rapid diversification as an explanation for the patterns found in the groups under study are accumulating in literature (e.g. Richardson & al., 2001a; Richardson & al., 2001b; Rüber & al., 2003; Beheregaray & al., 2004; Cieslak & al., 2005; Nosil & Crespi, 2006; this thesis, chapter 4). However, the term (adaptive) radiation is often used uncritically for almost any historic increase in numbers of taxa and this threatens the explanatory power of the term (Skelton, 1993). Furthermore, it is often stated that some organismal group had the built-in tendency to radiate and proliferate (perhaps because of some presumed key-character) when merely it is observed in retrospect that it had done so (Raikow, 1988). No causal relationship between the observed character and the diversification of the group is established. This usage is partly the result of the fact that still no consensus exists on how to define a radiation. However, understanding the processes responsible for radiations and detecting if radiations occur frequently can help us to better asses its importance in the evolution of the current flora and fauna and the origin of biodiversity in general.

The meaning of "radiation"

One of the definitions of radiation is *the evolution of a relatively large, monophyletic group of species or higher taxa within a relatively short period of time* (adopted from Gittenberger, 2004). If character and/or ecological divergence occurs in addition, the radiation can be called adaptive, otherwise it is non-adaptive (Gittenberger, 1991; Sanderson, 1998). The result of a radiation is a (sometimes large) difference in species numbers between the radiating clade and its non-radiating sister-clade.

In general, differences in species numbers can arise for four different reasons (Brooks & McLennan, 2002; Sudhaus, 2004). Firstly, the asymmetry can develop stochastically and no special factors are responsible for the pattern found (e.g. a geological hotspot facilitating plain allopatric speciation). Secondly, successful colonization of a new region devoid of species with similar modes of life (a founder event) can lead to asymmetry in the number of species. Thirdly, survivors of (mass-) extinctions (a bottleneck event) may be the source of numerous new species because of the disappearance of competitors and antagonists. Lastly, intrinsic factors such as key-innovations (a character that increases diversification rate or decreases proneness to extinction) are responsible for the extensive diversification of a group of organisms. In the first three scenarios the founders of a radiation can be regarded as relatively unspecialized, whereas in the fourth case they are specialized

(Sudhaus, 2004). Therefore, only the fourth factor would constitute an adaptive radiation. This is not a trivial distinction because “adaptive” is about character evolution and “radiation” is about speciation (Brooks & McLennan, 2002). Lineage diversification (speciation and extinction) and character diversification (morphological and ecological) should therefore be decoupled (Sanderson, 1998; although, inference mistakes can arise if the decoupled characters shaped the phylogeny under study, Maddison, 2006). In a radiation of species many new species arise in a short period of time (e.g. flowering plants; Willis & McElwain, 2002). On the contrary, a radiation of adaptations leads to the origin of many characters in a short period of time (for examples of adaptive radiations in plants see Classen-Bockhoff & al., 2004). The net number of lineages arising from a radiation of adaptations is not very important and adaptive radiations can therefore contain a relatively small number of species (e.g. the adaptive radiation of 28 species of Hawaiian Silverswords; Schluter, 2000).

Problems with the definition of radiation

Questions about the diversity of evolutionary groups are questions about variation in speciation and extinction rates, which leave their signatures in the shapes of phylogenetic trees (Mooers & Heard, 1997). Especially dated phylogenies are of great help in studying the tempo and mode of evolution (Richardson, 2001b). If in such a tree, many lineages arise in a short period of time, it might be concluded that a radiation has taken place. However, this conclusion is highly dependent on the meaning of the vague concepts “many lineages” and the definition of “a short period of time” (Gittenberger, 2004).

Especially at lower taxonomic level it is obvious that the concept “many lineages” is not clearly defined. Here “many lineages” is often translated as “species-rich”. The term “species-rich” has been widely used and covers a broad range between for example 62 species of *Camissonia* in Onagraceae (Levin & al., 2003), 100 species in the snapping shrimp genus *Synalpheus* (Morrison & al., 2004), 150 species of *Phylica* (Richardson & al., 2001b), 300 species of *Inga* (Pennington, 1997) and 2000 species of *Euphorbia* and *Carex*. These taxonomic patterns would only be comparable if the taxonomic units are equivalent, which they may not be. For distantly related clades, such as within eutharians, this has been shown not to be the case (Avise & Johns, 1999; Purvis & Hector, 2000). But even within angiosperms, different workers may adopt different concepts of species, with ages of taxonomic units being uncomparable. To get around the confounding issue, phylogenies allow to make comparisons of sister clades, which by definition are of the same age.

Next to this, the amount of time that is considered “short” for a radiation to take place is also arbitrary. For paleontologists a radiation takes places within some tens of millions of years at a macroevolutionary scale (Erwin, 2006). However, on microevolutionary scale the term radiation has been applied to time frames of 10 million years in the case of *Inga* (Richardson & al., 2001a), for 3 million years when the most recent common ancestor of the Galápagos finches colonized the Galápagos islands (Grant & Grant, 1996), or a period as short as 100,000 years in cichlid fishes (Verheyen & al., 2003). “Short periods” can only be defined in relation to the life-history traits of the group under study (e.g. length of life cycle). Again, this term is only meaningful in the context of closely related groups.

Therefore, one should always study the evolutionary context of a clade when trying to determine if that clade has radiated or, in other words, is unusually species-rich. This requires comparison to all closely related clades and a single comparison with another group is insufficient basis for judgement (Sanderson & Donoghue, 1996; Magallon & Sanderson, 2001; Losos & Miles, 2002). Sistergroup comparison is a useful tool for this because sister clades are monophyletic, comparable in most basic aspects of their biology and of the same age. It is the evolutionary equivalent of a control in experimental manipulations: if differences between sistergroups are found, there is evidence for differential rates of diversification in one group over another. Only then questions about underlying processes can be asked (Brooks & McLennan, 2002). The fact that sistergroups are of the same basic biology and age eliminates the possibility that one clade is more species-rich than the other simply because it has a very different biology or is older (Brooks & McLennan, 2002; Losos & Miles, 2002).

The use of sistergroups therefore resolves the two above mentioned problems. Comparing sistergroups redefines evolutionary success (i.e. species-richness) in terms of relative size rather than absolute size (Raikow, 1988; Slowinsky & Guyer, 1993) and rates of speciation and extinction are examined in the context of their relative and not absolute ages (Raikow, 1988). Furthermore, the use of sistergroups eliminates rank based and other taxonomic artefacts (Sanderson, 1998) thereby eliminating any investigator bias in the choice of groups for comparison (Brooks & McLennan, 2002). Because the use of sistergroup comparison is essential to radiation research, the definition of radiation will be extended and defined as the evolution of a relatively large, monophyletic group of species or higher taxa within a relatively short period of time, *compared to closely related monophyletic (sister)groups*.

Annonaceae as a model for radiation research

The avalaible phylogenetic data on Annonaceae (Mols & al., 2004; Pirie & al., 2006; Chatrou, & al., in prep; Erkens & al., chapter 2) and dates for all the clades in the family (Pirie & al., in prep) can be used to study diversification patterns in order to identify factors that drive speciation and the evolution of morphological (key-)characters in the family. For example, one of the most conspicuous features of the Annonaceae phylogeny is the difference between the so called Long Branch Clade (LBC) and Short Branch Clade (SBC; Richardson & al., 2004). This informal naming reflects the seemingly different rate of molecular evolution between these clades. As age estimates of the crowns of the two clades are similar (Richardson & al., 2004), the differences in evolutionary rates have led to significantly different average branch lengths from the common ancestors to the terminals (Richardson & al., 2004). The LBC and SBC together comprise the majority of genera and species in the family. The LBC and the SBC consist of approximately the same number of genera but the amount of species is different. Within the SBC one can find c. 50 genera comprising some c. 700 species in total. The LBC also contains c. 50 genera. These include the 10 largest genera of the family, some 1000 species together, and c. 40 smaller genera that contain the remaining 500 species.

The Annonaceae phylogeny offers two sources of information relevant to the study of (differences in) diversification rates in its clades: the topological distribution of species diversity across branches, and the temporal distribution of branching events through time (Sanderson & Donoghue, 1996). This article uses both topological and temporal methods to analyse the phylogenetic patterns found in Annonaceae. The primary goal is to pinpoint radiations of species. To this means, clades that show significant shifts in diversification rate are identified. This knowledge is then in a crude manner coupled to overall morphological data or (geological) events happening at particular points in time, to investigate whether any single factor or simple combination of factors might be associated with major rate shifts in the family.

MATERIAL AND METHODS

Phylogeny reconstruction

Phylogenetic relationships were obtained via a supermatrix method by Chatrou & al. (unpublished data) based on data from Pirie & al. (2006), Chatrou & al. (unpublished data), and Erkens & al. (chapter 2). One of the most parsimonious trees from this analysis was chosen and taxa were pruned so that only one species per genus was left (serving as "place-holder" for the genus), except in the case of a (possible) paraphyletic constitution when two species per genus were retained (figure 1). This was done to correct for bias in clade composition due to the different amounts of species sampled per genus. Because the resulting topology is derived from existing phylogenetic hypotheses, no in-depth discussion of recovered relationships will be given here (see Chatrou & al., in prep, for this discussion). Out of c. 130 genera 81 are represented in this study and no large genera were omitted from this analysis.

Species-richness data were taken from recent Annonaceae literature (see page 62 for overview and references). Where genera proved to be polyphyletic and no justification could be given for a particular distribution of numbers of species between the clades, the total species diversity was distributed equally over the different clades.

No complete species-level phylogeny for Annonaceae exists and with the topological method no correction is possible for the amounts of species per place-holder. For this reason the method cannot be used to investigate species-level diversification patterns, only genus level analyses can be conducted. Therefore, also a second (temporal) method was applied that can account for the amounts of species represented by the place holder taxon.

Topological method

A measure for imbalance in species numbers per node in a tree was proposed by Slowinsky and Guyer (1993). Using a general equal rates Markov (ERM) random branching process (Yule, 1924) as a null model, the probability of observing an equal or greater difference in species-richness between two sister clades is given by $2r/(r+s-1)$. Here s depicts the numbers of species in the species-richer clade and r in the species-poorer clade. A significant difference in sister-group diversity constitutes rejection of the ERM null model, and therefore, suggests that the two clades have diversified at significantly different rates (Slowinsky & Guyer, 1989a; 1989b; Slowinsky, 1990). Slowinsky and Guyer's method has been criticized for low power (Sanderson & Donoghue, 1996), poor accuracy (McConway & Sims, 2004), and false inference of rate shifts in descendant nodes, the so-called "trickle-down" effect (Moore & al., 2004; for an analytical rejection see: Vamosi & Vamosi, 2005). To overcome these shortcomings, the model has been extended from individual nodal probabilities to whole-tree tests (Chan & Moore, 2002; Moore & al., 2004). These tests of diversification rate variation are based on cumulative ERM probabilities and outcomes are

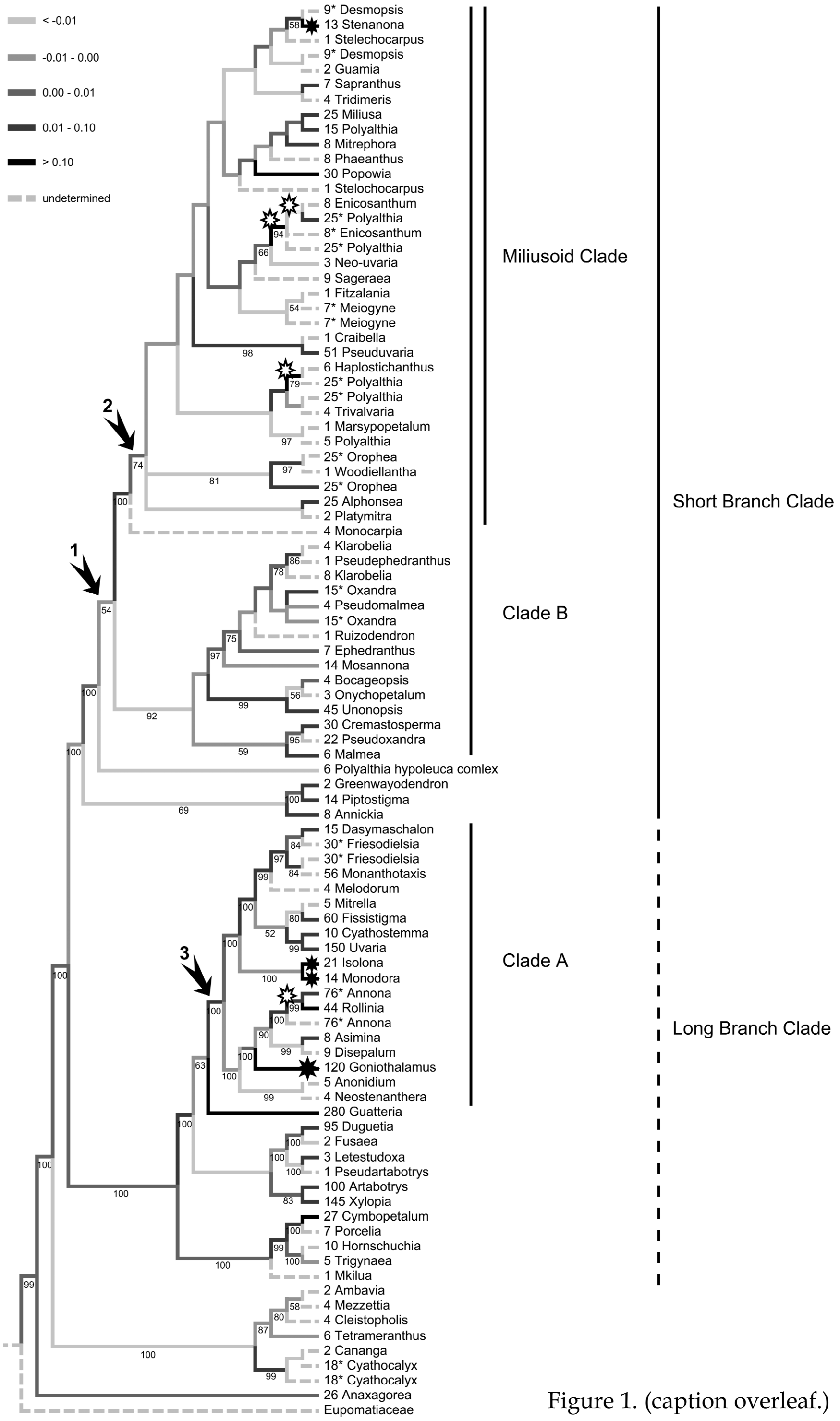

Figure 1. (caption overleaf.)

reported as *M* statistics (M_Σ M_Σ*, M_Π and M_Π*). The obtained *p*-values are called ERM nodal probabilities.

The *M* statistics are intended to provide differential sensitivity to asymmetry arising at different phylogenetic scales (i.e. the relative nodal depth in the tree), permitting their application to a corresponding range of associated evolutionary processes (Moore & al., 2004). The type of diversification rate variation to which each statistic is most sensitive is determined by the manner in which it summarizes information from individual nodes. M_Σ and M_Π both consider the relative asymmetry of all internal nodes (Chan & Moore, 2002). They are based on the cumulative ERM probability derived from the product (M_Π) and the sum (M_Σ) of individual nodal probabilities (Chan & Moore, 2002). However, M_Π and M_Σ show differential sensitivity to large scale asymmetry. This is because of the fact that the smallest nodal probabilities can only be generated by large-scale asymmetry (i.e. the potential magnitude of differences in species diversity is greater at more inclusive nodes). Small probabilities will therefore have a relatively large effect on M_Π because calculation of the statistic involves multiplication of individual probabilities. In contrast, M_Σ sums nodal probabilities, such that the impact of such small probabilities is greatly diminished, thus allowing nodal probabilities associated with small scale asymmetry to make a more equable contribution to the whole-tree probability (Chan & Moore, 2002). M_Π* and M_Σ* are whole-tree statistics that are weighed by the size of their corresponding node. Because larger nodes are realized deeper in the tree, they are more sensitive to diversification rate variation at larger phylogenetic scales (Moore & al., 2004). In behaviour, M_Π* and M_Σ* are similar to their non-weighed counterparts. Therefore, the relative sensitivity of the different statistics to large-scale diversification rate variation is $M_\Sigma < M_\Sigma^* < M_\Pi < M_\Pi^*$ (Moore & al., 2004).

This method eliminates the confounding effect of different clade ages by comparing only sister groups.

The computer program Symmetree v1.1 (Moore & al., 2004) was used to test for significant diversification rate variation and to locate significant shifts in diversification rate among branches of the Annonaceae tree. The program does not require branch lengths estimates, which eases the analysis of phylogenies for which such data are unreliable or unavailable, such as supertrees.

Statistical testing for significant whole-tree diversification rate variation was through Monte Carlo simulation of the null distribution using 1,000,000 tree topologies with the same number of taxa as the tree in figure 1, but generated under an ERM model. Three polytomies are present in the topology of figure 1. These were not resolved a priori because this can lead to inflated imbalance, especially when the topology is chosen arbitrarily

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Figure 1 (previous page). Concise Annonaceae topology derived from Chatrou & al. (in prep). One of the most parsimonious trees from this analysis was chosen and taxa were pruned so that only one species per genus was left, except in the case of a (possible) paraphyletic constitution when two species per genus were retained. Bootstrap percentages are indicated below the branches (only values >50% are shown). Amounts of species per place holder taxon are indicated before its name. Asterisks (*) indicate poly- or paraphyletic taxa for which the number of species has been equally distributed over the constituent lineages due to the unavailability of a trustworthy estimate of species numbers per clade. Significant Δ rate shifts are indicated with a numbered arrow (numbers correspond to branches mentioned in table 2) and significant LogN rate shifts are indicated by a solid star (terminal branches included) or an open star (terminal branches excluded; details in table 3).

(Mooers & al., 1995; Heard & Mooers, 1996). Because these polytomies reflect the lack of resolving power of the data, they were treated as "soft" in the analyses (i.e. phylogenetic uncertainty instead of actual simultaneous multiple branching events). Most and least symmetric resolutions of all possible dichotomous resolutions were analytically calculated. These maximum and minimum symmetry values provide the confidence interval for the range of possible outcomes (Chan & Moore, 2005).

Shifts within more nested clades can influence estimates obtained from more inclusive clades (i.e. they are larger because of the larger nested clade), thus somewhat confounding the inference of diversification rate variation (Moore & al., 2004). Therefore, the analysis was carried out for the tree as a whole but also for the SBC and LBC separately to investigate if this phenomenon occurred.

The M statistics provide an answer to the question whether or not a given tree has experienced significant shifts in diversification rate. However, they cannot indicate where in the tree these shifts have occurred. Therefore, Δ_1 and Δ_2 shift statistics were calculated (Moore & al., 2004). These statistics indicate the probability of a diversification rate-shift along an internal branch of a local three-taxon tree comprising a local outgroup and the two basal-most ingroup clades. The three-taxon evaluations are iterated over all internal branches to effectively survey the whole tree for diversification rate shifts (Moore & al., 2004). The Δ_1 shift statistic calculates the difference in likelihood ratios between homogeneous and heterogeneous models, assessed at the inclusive and nested nodes (exact explanation and calculation in Moore & al., 2004) and the Δ_2 shift statistic is a more complicated version of Δ_1 (Moore & al., 2004).

Statistical testing of Δ was achieved by means of Monte Carlo simulation of its null distribution, using 1,000,000 tree topologies of the same size as the input tree, but generated under an ERM model. Where either the ingroup or outgroup nodes in the three-taxon set contained a polytomy, the analyses were repeated for each possible resolution, giving an upper and lower bound on the probability value obtained (Chan & Moore, 2005).

For comparison two often used tree-shape indices are reported as well. I_C (Colless' index; Colless, 1982; Heard, 1992) is the most commonly used index. I_C sums over all (n-1) nodes in a tree with n tips, the difference in the number of tips subtended by the right-hand and left-hand branches arising at each node, and then normalizes by dividing by the largest possible score (calculated as $(n-1)(n-2)/2$; Mooers & Heard, 1997). It is a measure for tree imbalance, where $I_C=0$ for a perfectly balanced and $I_C=1$ for a perfectly imbalanced tree (i.e. higher values indicate a more imbalanced tree; Mooers & Heard, 1997). B_1 (Shao & Sokal, 1990) is a balance index and is the most powerful of the previously proposed balance indices (Kirkpatrick & Slatkin, 1993). For each of the interior nodes (except for the root of the entire tree) the maximum number of other nodes between that node and a tip it subtends (M_j) is determined (Mooers & Heard, 1997). B_1 is then calculated as: $S_j\ (1/M_j)$, where $j = 1, 2, ..., n-1$ but $j \neq$ root (Shao & Sokal, 1990). B_1 is larger for more balanced trees (Mooers & Heard, 1997). I_C and B_1 measure different aspects of balance. I_C takes the position or size of nested clades into account, while B_1 only measures the maximum distance from a local root to a subtended terminal (without allowing for the size of each nested clade; Shao & Sokal, 1990). As result of the different calculation methods, I_C and B_1 are sensitive to

Table 1. ERM nodal probability values corresponding to tests of ERM cladogenesis in major Annonaceae clades as derived from Monte Carlo simulation of the null distribution for each statistic (specifications as explained in the text). Uncertainty associated with polytomies was assessed by investigating all possible alternative combinations of dichotomous resolutions, providing the upper and lower bounds of the confidence interval (the "high" and "low" values for high and low symmetry). These bounds correspond to the tail probabilities for the 0.025 and 0.0975 frequentiles, respectively. For the LBC no confidence interval was calculated because this tree was completely resolved and therefore singular values for this topology are indicated in the "high" row. The sensitivity of the whole-tree statistics to large scale diversification rate variation increases to the right across a given row (i.e. the sensitivity of $B_1 < M_\Sigma < M_\Sigma^* < M_\Pi < M_\Pi^* < I_C$). Resolution was calculated as k/(n-1), where k is the number of nodes in a tree of n tips; this value implicitly assumes that the underlying tree is strictly dichotomous (i.e. all polytomies are "soft").

clade	tree size	resolution	B_1	M_Σ	M_Σ*	M_Π	M_Π*	I_C
			high **low**	**high** **low**	**high** **low**	**high** **low**	**high** **low**	**high** **low**
Total	96	98	0.19082	0.00155	0.00006	0.00003	0.00000	0.00007
			0.59265	0.12215	0.08027	0.04316	0.02823	0.00382
LBC	31	100	0.96807	0.43994	0.30434	0.36617	0.26524	0.30244
SBC	55	94	0.05638	0.00134	0.00045	0.00019	0.00015	0.00099
			0.19143	0.04268	0.03018	0.01326	0.00842	0.00495

imbalance at different phylogenetic scales. B_1 is more sensitive to imbalance near the tips of the tree and I_C is more sensitive to large scale imbalance. The sensitivity of all discussed whole-tree statistics to large scale diversification rate variation increases from B_1 via M_Σ , M_Σ* , M_Π , M_Π* to I_C. Inconsistencies between the I_C, B_1 and M statistics do not indicate faults of the indices but reveal the fact that they embody different definitions of imbalance (Shao & Sokal, 1990).

Temporal method

The formula Log(N)/t was applied to estimate net diversification rates (R) for each clade, where N is the number of species within a clade and t is the absolute time since that clade diverged from its sister (Isaac & al., 2003). Shifts in diversification rates per branch were assessed. This was done by subtracting the R value of the stem node from that of the crown node of a branch (Isaac & al., 2003; Davies & al., 2004). This resulted in a maximum likelihood estimate of shift in

Table 2. Branches that show significant rate shifts ($p < 0.05$) as indicated by two likelihood ratio-based shift statistics (Δ_1 and Δ_2; as explained in the text). Shift statistic values indicate the probability of a diversification rate-shift along an internal branch. Δ_1 and Δ_2 were calculated on the basis of the total tree, and the Short Branch Clade (SBC) and Long Branch Clade (LBC) subtrees. Shifts are indicated in figure 1 by a numbered arrow (numbers correspond to the branches in the table below).

Branch	**Δ_1**	**Δ_2**	**Rate-shift at branch leading to**
Total tree and SBC subtree			
1	0.01735	0.02489	Clade B
2	0.04603	0.05901	Millusoid clade
Total tree and LBC subtree:			
3	0.02339	0.03509	Clade A

diversification rate (LogN) rate shifts (Davies & al., 2004). This method shows rate changes per branch in the tree and makes it possible to identify the clades with the biggest positive or negative changes in rate. Furthermore, when average shifts in R are plotted against the age of the nodes in the tree it is possible to investigate if during any particular time window significant shifts in R have occurred.
This method uses absolute time estimates and therefore dates for all nodes in the phylogeny were taken from Pirie & al. (in prep; see article for discussion on dates). Genera for which no crown group age could be estimated (because of the presence of only one accession in the dated tree) were not assigned an age.

Whether diversification rates were conserved among close relatives was tested with the use of randomisation tests. Species numbers of genera were randomised 100 times among the tips of the tree. For each randomisation trial, R per node was recalculated as well as the sum of all LogN rate shifts between the stem and crown node of a branch. If diversification rates were conserved among close relatives, the sum of observed shifts in diversification rates across the tree should be lower than among random trials shuffling species numbers among genera.

Characters correlated with biotic and abiotic rate shifts
Possible correlation of the evolution of characters from leaf architecture (Johnson, 2003), leaf anatomy (van Setten & Koek-Noorman, 1986), flower and fruit morphology (Koek-Noorman & al., 1997), chromosome numbers (Morawetz & Waha, 1985), anther development (Tsou & Johnson, 2003), pollination characteristics (Gottsberger, 1999), evolution of fragile exines (Waha, 1987), pollen characters (Doyle & Le Thomas, 1997a), and oil composition (Maia & al., 2005a; Maia & al., 2005b), were explored with shifts in diversification rates in Annonaceae. No comprehensive study of all possible factors influencing diversification in Annonaceae is given but rather a simple survey to explore whether any single factor or simple combination of factors might be associated with major rate shifts in the family.

RESULTS

Topological method
To detect if the Annonaceae tree shows significant imbalance in tree shape, ERM nodal probabilities (*M* statistics) were calculated as well as I_C and B_1 indices (table 1). The smallest *p*-values obtained for the tree in figure 1 were returned by M_Π, M_Π* and I_C suggesting that significant diversification rate variation occurred at intermediate to larger phylogenetic scales (i.e. not near the tips or at the root of the tree). The Δ_1 and Δ_2 shift statistics (table 2) reveal the locations of three significant diversification rate shifts in the history of Annonaceae at this intermediate scale (indicated in figure 1 with an arrow). The first occurred within the LBC at the origin of a strongly supported clade (arrow #3), here referred to as Clade A (containing the *Annona*-group, *Isolona* and *Monodora* and a clade consisting of species with a climbing habit). The second rate-shift occurred in the SBC at the base of a strongly supported clade that accommodates almost all genera of the SBC (arrow #1), except for the African *Annickia-Piptostigma-Greenwayodendron*-clade and the Southeast Asian *Polyalthia hypoleuca* complex (a well circumscribed clade on the basis of molecular data and bark, leaf and seed characters; Mols & al., 2004). This restricted SBC will from here

Table 3. Significant increases and decreases (95% confidence level) in diversification rates (LogN) including and excluding terminal branches. The respective nodes are indicated in figure 1 by a star. Nodal support values were obtained from Chatrou & al (in prep). Bracketed values behind clade names when terminal branches are excluded indicate the position of the rate-shift in the rate-shift ranking when terminals are included.

	Rate shift (+: positive, -: negative)	Diversification rate-shift at branch leading towards	Age (my)	Number of species in clade	Node support (Bootstrap)	Geographical distribution	Putative key innovation/ diversification influencing factor
Terminal branches included*	+ 0.39266	*Goniothalamus*	4.49	120	100	Southeast Asia	?
	+ 0.32587	*Stenanona*	2.86	13	89	Central America	?
	+ 0.25576	*Isolona*	4.04	21	100	Africa & Madagascar	syncarpy
	+ 0.24952	*Monodora*	3.57	14	100	Africa	syncarpy
	+ 0.14148**	*Guatteria*	11.87	280	100	Central and South America	unspecialized
Terminal branches excluded*	+ 0.13601	*Enicosanthum-Polyalthia* s.l. clade (7***)	20.75	66	94	Southeast Asia	?
	+ 0.12279	*Haplostichanthus-Polyalthia* clade (8***)	7.79	31	79	Southeast Asia	?
	+ 0.06429	*Annona-Rollinia* clade (14***)	17.33	194	100	Central and South America, Africa	syncarpy
	- 0.08245	*Enicosanthum-Polyalthia* s.s. clade (1***)	10.68	33	--	Southeast Asia	--

* Terminal branches included: average: 0.022313, s.d.: 0.061589; terminal branches excluded: average: 0.004612, s.d.: 0.027794.

** Guatteria has the fifth largest rate-shift when terminal branches are included but this shift is marginally non-significant. The genus is included in this table because it is the largest Annonaceae genus.

*** These rate shifts are not significant when the terminals are included.

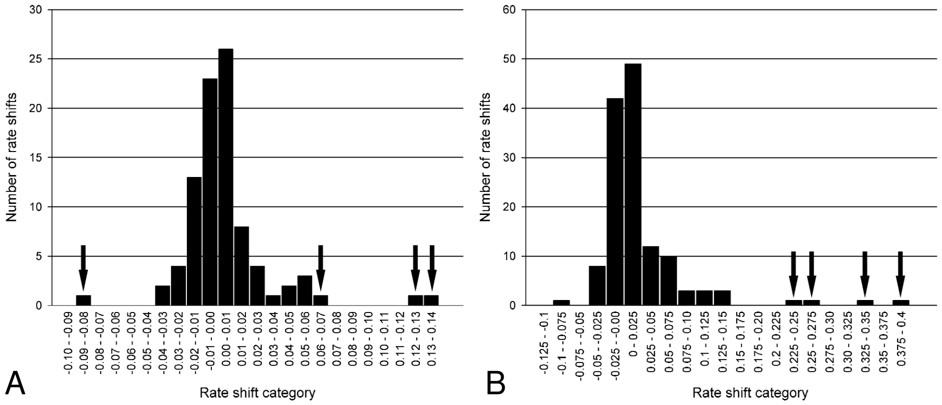


Figure 2. Number of rate shifts per rate shift category plotted against the total number of observed shifts in diversification rate for the tree in figure 1. The arrow indicates significant rate shifts (details in table 3). A. internal branches only, B. internal branches and terminals.

on be referred to as Clade B. The third shift in diversification rate occurred at the base of the moderately supported Miliusoid Clade (arrow #2; Mols, 2004), although this shift is marginally non-significant for Δ_2.

The three different analyses (whole tree, SBC only and LBC only) proved to be insensitive to the specification of taxonomic scope (table 2) because all Δ_1 and Δ_2 analyses yielded the same result (i.e. irrespective of whether the analysis was applied simultaneous to the whole tree or separately to the SBC or LBC). This indicates that shifts within more nested clades did not influence estimates obtained from more inclusive clades.

Temporal method

Significant increases and decreases in diversification rates could be identified because the temporal measure includes the direction of each shift as well as its magnitude. When only internal branches were looked at, three branches showed a significantly raised diversification rate when compared to all other branches ($p<0.05$; figure 1, opens star, figure 2A; table 3) and one branch had a significant slowdown in rate ($p<0.05$; figure 1 open star, figure 2A; table 3). However, this slowdown occurs along a branch that is unsupported and towards a clade to which the number of species was assigned arbitrarily. When terminal branches were included, the previously mentioned rate shifts were non-significant but shifts in diversification rate along several terminal branches were ($p<0.05$; figure 1, solid star, figure 2B; table 3). The branches leading towards the crown groups of *Goniothalamus*, *Stenanona*, *Isolona*, and *Monodora*, respectively, showed significant increases in diversification rate (table 3), much larger than the significant increases when terminal branches were excluded. The largest genus in the family, *Guatteria*, showed a marginally non-significant increase in diversification rate. No significant slowdown in rates was observed in this second analysis.

The branch leading towards the SBC as a whole shows a negative rate-shift (-0.003410) and the branch subtending the LBC shows a positive rate-shift (0.003738) but these shifts are not significantly different from the average shift in rate (figure 2). The same is true for the

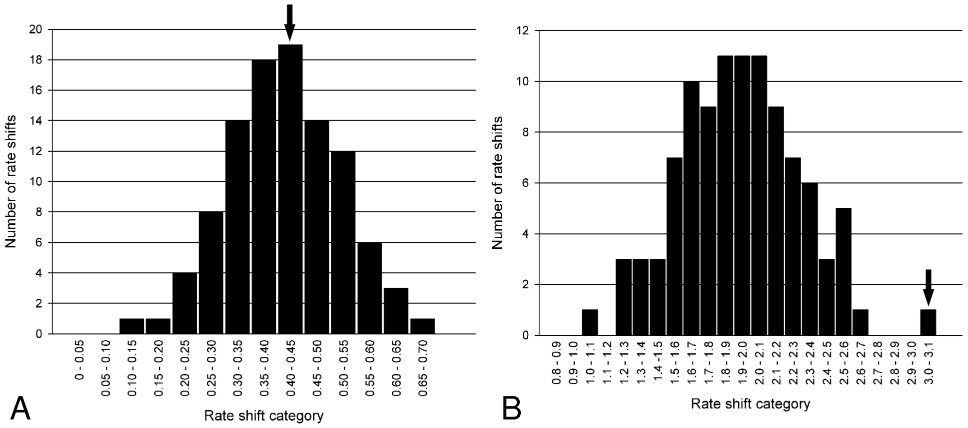


Figure 3. Results of randomization tests conducted to test if LogN rate-shifts were phylogenetically conserved (specifications as explained in the text). The number of summed shifts in diversification rate per rate-shift class is shown. The arrow indicates the class containing the sum of rate shifts for the tree in figure 1. A. internal branches only, B. internal branches and terminals.

branches subtending the *Anaxagorea* clade (0.008704) and the *Ambavia*-group with *Cananga* (-0.012310; $p<0.05$; terminal branches included: average: 0.022313, s.d.: 0.061589; terminal branches excluded: average: 0.004612, s.d.: 0.027794; see also figure 2).

The detected diversification rates were not significantly phylogenetically heritable between related lineages when the terminals were excluded, as show by the randomization tests. The sum of rate shifts for the tree in figure 1 (0.415113) was not significantly different from the randomised rate shifts (average: 0.364339; s.d.: 0.106862; $p<0.01$, figure 3A). This means that sister clades are *not* more likely to have similar species numbers than two clades chosen at random. Furthermore, when branches leading to the crown group of genera of which the age could be determined were included, the sum of rate shifts for the tree in

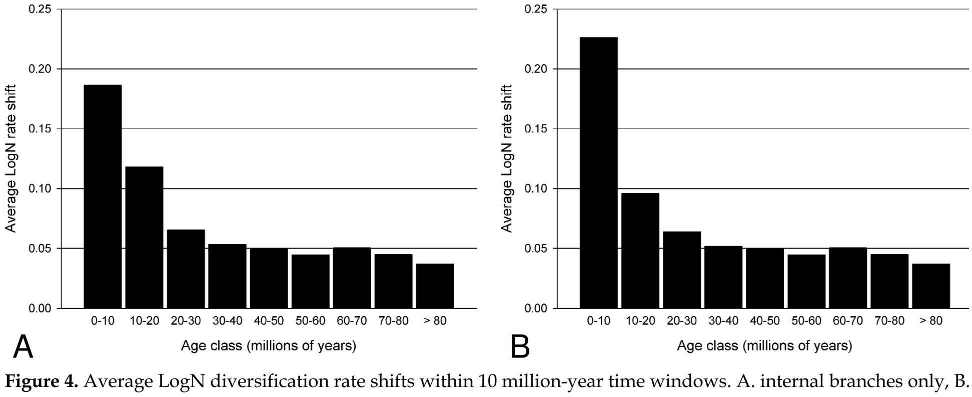


Figure 4. Average LogN diversification rate shifts within 10 million-year time windows. A. internal branches only, B. internal branches and terminals. Dates of nodes were estimated by Pirie & al. (in prep). Average changes in diversification rates increase with decreasing age (r=-0.79 and r=-0.72; for figures 4A and 4B respectively; r = correlation coefficient). Only within the most recent time frame the average rate shift is significantly higher than the average shift over all time windows ($p<0.05$).

figure 1 (3.012272) was significantly higher than those from the randomised rate shifts (average: 1.825309; s.d.: 0.348024; $p<0.01$, figure 3B). Lower values are expected in comparison to randomized tests when rates are phylogenetically heritable between related lineages, thus both randomization tests indicate that no phylogenetically heritable component is present in the shifts in rate in Annonaceae.

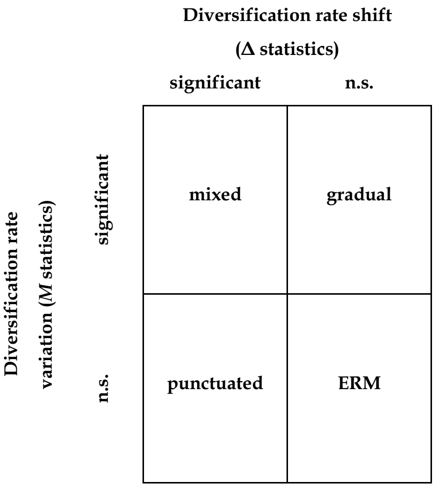
When a correlation coefficient (r) is calculated, it is clear that average diversification rate shifts within Annonaceae have been increasing from past to present (r=-0.79 and r=-0.72; figure 4A and 4B). The most recent time frame shows a significantly higher average shift in diversification rate (with and without terminal branches included) than any other time frame.

DISCUSSION

Imbalance and shifts in diversification rate can be used to study the evolutionary process. One could for instance hypothesise that the radiation of a clade results in an imbalanced tree or that the branch leading towards a radiating clade exhibits a higher diversification rate in comparison to a clade that has not radiated (Sanderson & Donoghue, 1994). After identifying radiating clades, (a)biotic explanations can be sought for the observed patterns in (im)balance (Mooers & Heard, 1997).

Radiations in Annonaceae: comparison of rate-shift analyses

Analysis of the supertree revealed significant imbalance in net diversification rates among Annonaceae lineages compared to the null model that all lineages have an equal diversification rate (table 1). This result from the topological analysis shows that the tree in figure 1 is imbalanced and that this imbalance mainly can be found in the SBC (table 1). The Δ_1 and Δ_2 shift statistics (table 2) further show that these shifts occurred along the branch leading to the Miliusoid Clade, and along the branches leading to Clade A and Clade B (figure 1). No significant imbalance is found towards the tips of the tree. The M statistics did not indicate any significant among-lineage diversification rate variation in the LBC but the Δ_1 and Δ_2 shift statistics did locate a significant diversification rate shift. This is due to the fact that the diversification rate heterogeneity was restricted to a single branch (figure 1; base of Clade A), constituting a significant local rate-shift that was below the threshold of detection under the whole-tree M statistics (Moore & al., 2004). This single rate-shift was insufficient to cause rejection of the null hypothesis that the LBC as a whole diversified under a stochastic ERM branching model.



Diversification rate variation (*M* statistics)	Diversification rate shift (Δ statistics): significant	Diversification rate shift (Δ statistics): n.s.
significant	**mixed**	**gradual**
n.s.	**punctuated**	**ERM**

Figure 5. M statistics together with Δ rate shift statistics can be used to explore modes of diversification. The four scenarios involve rate heterogeneity consistent with either mixed, gradual or punctuated evolutionary models of cladogenesis, or stochastically homogeneous (ERM) diversification rates (adopted from Moore & al., 2004).

In terms of modes of diversification, the pattern in the LBC points towards a single punctuated cladogenesis event (figure 5; Moore & al., 2004) at the base of Clade A. The SBC is overall more significantly imbalanced and two significant Δ rate shifts are detected, indicating a mixed evolutionary model of cladogenesis (figure 5; Moore & al., 2004).

Conversely, the temporal method indicates that nodes in more recent time periods tended to display a greater LogN rate-shift than expected under the null model (figure 1 and figure 4B; table 3). An explanation for this pattern might be that genera were used as terminals. Shifts that were reconstructed as occurring along the stem branch of a genus could have actually occurred within the genus. But because of the use of place-holder taxa these shifts could only be reconstructed along the stem branch of the genus. This bias would not affect reconstructed shifts in diversification rates at nodes deeper in the tree (Davies & al., 2004). To test for the influence of this interfering factor the analysis was also conducted without the terminal branches included (figure 4A). This yielded the same result suggesting that the use of genus level analysis was not a disturbing factor.

An alternative explanation could be the fact that two sister clades with balanced species numbers were joined by a relatively long stem branch. This would lead to the reconstruction of a high rate in both sister clades compared to the rate expected for their nesting clade, a situation not recognizable from topology alone (Davies & al., 2004). This might for instance be the case for *Isolona* and *Monodara.* The branch leading to this clade is relatively long (this thesis, chapter 2) and both genera are reconstructed as having a significant rate shift (table 3). Also for *Goniothalamus* and *Guatteria* long branches subtend the both clades. The significant rate shifts obtained with the temporal method might therefore be influenced by this confounding factor and should be interpreted with care.

Because both the topological and temporal method indicate different nodes (or branches) as showing significant shifts in diversification rate, it might be concluded that the results from both methods contradict each other. However, one has to keep in mind that both methods indicate different aspects of the information available from a cladogram. The topological method solely uses tree topology (the branching pattern of a tree) to study the balance (the extent to which nodes define subgroups of equal size) of that tree. It ignores branch length information and size of the terminal taxa. The temporal method encompasses, next to balance, also the distribution of branch lengths (i.e. absolute clade age) over the tree. The combination of topology and branch length information is usually referred to as tree shape (Mooers & Heard, 1997). Often temporal models are held over topological methods because they directly incorporate information on the timing of diversification (Chan & Moore, 2005). On the other hand, because topological methods effectively ignore temporal information, topology-based statistics might be more reliable for the inference of diversification rate shifts in supertrees (for which reliable age estimates are sometimes difficult to obtain). As can be seen here, a combination of these two methods of analysis can yield additional information on the evolutionary patterns under study.

Doyle & Le Thomas (1997b) have hypothesised that Annonaceae have radiated in proto-Africa and proto-South America in the late Cretaceous. Furthermore, Raven & Axelrod (1974) as well as Richardson & al. (2004) mention the possibility that Annonaceae have radiated extensively in tropical Asia by the Palaeogene. This study confirms the latter but not the former idea by showing that Clade A, Clade B and the Miliusoid Clade indeed are Palaeogene radiations, as illustrated by shifts in diversification rate at the base of these clades (figure 1). Richardson & al. (2004) additionally postulate that c. 20% of the African species within the SBC are comparatively recently derived as a result of radiations following long-distance dispersal. However, these so called radiations are not accompanied by shifts in diversification rate and therefore do not constitute a radiation but speciation not deviating from a stochastic ERM branching model. This pattern should be reinvestigated, however, when a better supported topology for this clade is available. Lastly, Richardson & al. (2004) state that the most rapid radiation has taken place in the Southeast Asian genus *Goniothalamus*. Indeed, this radiation is the most rapid and shows the largest shift in diversification rate within the family (table 3).

The LBC and SBC each contain approximately 50 genera but the amount of species is different (c. 700 vs. c. 1500 species for the SBC and LBC respectively). Additionally, the LBC includes the 10 largest genera of the family comprising c. 1000 of its 1500 species. The process behind this LBC-SBC difference is unclear. The topological method does not indicate any significant imbalance between the LBC and SBC. Furthermore, the temporal method indicates that the difference in species-richness is not attributable to an increase in diversification rate along the stem lineages of these clades. It uncovers a small increase in diversification rate at the base of the LBC and a small decrease at the base of the SBC, but both changes are not significant. The distribution of significant LogN rate shifts between these clades does differ. Four out of five largest increases in diversification rate have occurred within the LBC, only one in the SBC (and the latter in a poorly supported part of the tree, rendering this result questionable). However, these four radiations did not produce the bulk of the species present in the LBC. Of the 10 largest genera in the family (*Guatteria*, *Annona* (including *Rollinia*), *Uvaria*, *Xylopia*, *Goniothalamus*, *Artabotrys*, *Duguetia*, *Friesodielsia*, *Fissistigma*, and *Monanthotaxis*) only *Goniothalamus* constitutes a radiation of species. Furthermore, *Guatteria*, the largest genus in the family, does not (although only marginally non-significant) constitute a radiation. As a matter of fact, in relation to its sistergroup, *Guatteria* is the smallest of the two (290 *Guatteria* species vs. 737 for Clade A) and the genus might actually be seen as species poor.

In Annonaceae clade size is not a good predictor for the onset of a radiation and this study illustrates again that the size of a group of organisms is not a priori evidence that the group arose from non-random speciation and/or extinction (Slowinsky & Guyer, 1993).

Incomplete sampling could be a confounding factor with respect to the balance of the tree in figure 1. It has been shown that incomplete sampling will bias the outcome of the analysis because oversampled clades will tend to have shorter branches than will undersampled clades (Savolainen & al., 2002). This in its turn has an effect on the ease of reconstructing relationships and the dating of clades. However, this effect probably does not contribute to the apparent difference in branch lengths between the SBC and LBC. In the SBC 121 out of c. 700 species have been sampled (17%) and in the LBC 61 out of c. 1500 species (4%). The effect of species level sampling is not the problem, though, because analyses are carried out at genus level or above. However, 45 out of c. 50 genera in the SBC have been sampled (90%) while only 29 genera have been sampled in the LBC (58%). To investigate the effect of this, preliminary analyses of incomplete sequence data of 11 non-included small (African) genera have been carried out. These revealed no major topological changes (Couvreur, pers. comm.), since the new genera were placed within clades near the tips of the tree in the LBC, thus not influencing internal branch lengths at deeper levels.

Possible causes for radiations

It is interesting to relate diversification rate changes to possible biotic or abiotic triggers. Differences in species numbers between clades can be caused by four factors (Brooks & McLennan, 2002; Sudhaus, 2004): stochasticity, founder events, bottlenecks, or key-innovations. In the first three scenarios the founders of a radiation can be regarded as relatively unspecialised, where in the fourth case they are specialised (Sudhaus, 2004) and only fourth scenario therefore constitutes an adaptive radiation.

Invoking key-innovations is controversial. A key innovation can be defined as an aspect of the organismal phenotype that promotes diversification (there exist many other definitions, though; Hunter, 1998). The rationale is that a shift in diversification rate can be coupled to the evolution of a presumed key character along the same branch (Sanderson & Donoghue, 1994). However, these correlations should be made with great care, since traditionally this process simply entails identifying whichever feature of a group seems most distinctive (Slowinsky & Guyer, 1993). Furthermore, a lack of replication prevents statistical testing of the putative key innovation (Schluter, 2000). Even if replication is achieved it is possible that a character that is causally involved in increasing diversification rates in one clade, might not have the same effect in another clade (Brooks & McLennan, 2002). This because key-innovations by themselves are not sufficient reason for biological expansion, since evolution always occurs in a context (Hunter, 1998). No comprehensive study of all factors possibly functioning as key-innovations will be given here but rather a simple survey to pinpoint single (or a combination of simple) factors that might be associated with the detected significant rate shifts in the family.

The topological method indicates imbalance at the base of three clades. Clade A has one clear leaf architectural synapomorphy (Johnson, 2003). The whole clade has distichous trunk phyllotaxis (further only found in *Anaxagorea* and *Cleistopholis*) while the other genera have a spiral arrangement. For Clade B as a whole no clear synapomorphies exist. It is geographically structured, though. Next to a strongly supported Neotropical clade, it contains the Southeast Asian Miliusoid Clade at the base of which the third imbalance occurs. The Miliusoid clade is found to be separated from the rest of the SBC by several pollen characters. The miliusoid taxa have globose, cerebroid or echinate, disulcate pollen where the rest of the SBC has monosulcate, perforate to reticulare, boat-shaped pollen (Mols, 2004). The clade is not completely Southeast Asian because it contains a small clade of Central American genera (Richardson & al., 2004). Because of the geographic structure in the SBC, Clade B and the Miliusoid Clade might be species-rich as the result of a radiation after a founder event.

The temporal method indicates four significant rate shifts. The largest is along the stem branch of the Southeast Asian genus *Goniothalamus* (table 3) but the origin of this shift in diversification rate remains a mystery. No features of this genus would obviously qualify as a key innovation (Saunders, pers. comm.). For instance, none of the flower or fruit characteristics are that remarkable in terms of evolutionary innovations within Annonaceae. Additionally, although the topography of Southeast Asia (and especially its island archipelagos) is conducive to allopatric speciation, there is no obvious reason why *Goniothalamus* should diversify so much more rapidly than other genera in the same region. Annonaceae species, including *Goniothalamus*, often have very narrow distribution patterns. Interestingly, there is somewhat equivocal evidence to suggest that smaller geographic range size in birds is associated with higher rates of diversification (Isaac & al., 2003). This conclusion is opposite the general view that the probability of allopatric speciation increases with range size (Rosenzweig, 1978). The factor range size should be further explored to see if this ecological variable has any correlation with the patterns found in Annonaceae.

The second largest shift in diversification rate occurs along the stem towards the Central American genus *Stenanona* (table 3). This genus is part of a small 7 genera Central American clade that is embedded in the large Southeast Asian Miliusoid Clade. *Stenanona* can be found from Mexico (Veracruz) to Colombia (Nariño). In the field it is easily recognisable by the dramatically long drawn-out, aristate petal apices, a synapomorphy for the genus. This petal morphology, in combination with the pink to blood red coloured of the flower, is suggestive of a fly-pollination syndrome (Schatz, 1987). If so, this would be one of the few cases of non-beetle pollination in the family (Gottsberger, 1999) and perhaps a cause for the radiation of the genus.

The young crown-age estimate in combination with the size of the genus (13 spp.) lead to a high LogN estimate. However, the unsupported topology of this part of the tree in figure 1 warrants caution and further conclusions about this putative radiation should be postponed.

Two sister lineages, *Isolona* and *Monodora*, each separately show a significant increase in diversification rate (table 3). *Monodora* is wide spread from Sierra Leone to Angola across to Somalia to North South Africa. *Isolona* has a more restricted distribution but is present in Madagascar. *Monodora* and *Isolona* are unique and distinct from the rest of the family due to the presence of a truly syncarpous gynoecium (Deroin, 1997). With regard to morphology both genera are very different and without the syncarpous fruit synapomorphy their evolutionary relationship could easily be overlooked. *Monodora* has basally fused petals, pollen in tetrads and very conspicuous, orchid like, outer petals (the inner petals are small and cover the receptacle; Couvreur & al., in press). *Isolona* has petals fused up to $^1/_3$ of their length, pollen in monads (a reversal when compared to the other genera in the LBC), and not very conspicuous petals (inner and outer petals are of equal size; receptacle freely accessible; Couvreur & al., in press).

Both genera therefore have several characters that could be assigned as key innovation. Syncarpy is considered a key innovation (Endress, 2001) because it has several important evolutionary advantages over apocarpy especially at the pollination level. Syncarpy arose many times during angiosperm evolution (Armbruster & al., 2002) but remains rare in basal angiosperms limited to a few "aberrant groups" (e.g. Canellaceae and the genus *Takhtajania* (Winteraceae); Endress, 1982). Further investigation should therefore be conducted to establish which character(s) have causally promoted diversification in these genera.

One cautionary remark should be made. The above mentioned preliminary analyses of incomplete sequence data of 11 non-included small (African) genera, revealed no major topological changes. However, most of these unplaced species form a clade together with *Isolona* and *Monodora*. Thus, although there is no influence of these non-included genera on the results for the LBC as a whole, this particular clade is highly undersampled. Adding these unsampled genera would shed more light on the already mentioned effect that the long branch subtending this clade could have lead to the reconstruction of a high rate in both lineages in comparison to their nested clade.

Not many shifts in diversification rate have occurred in the evolutionary history of Annonaceae. The shifts that occurred are not easily linked to for instance key-innovations or geological events. Annonaceae are not the only group for which it proves difficult to correlate biotic and abiotic factors to shifts in diversification rate. Because of this difficulty there has been a recent renewal of interest in the hypothesis that cladogenesis may be random, or nearly random, with respect to the intrinsic biology of the organisms concerned (Ricklefs, 2003; Davies & al., 2004).

Given the large number of possible and biologically relevant alternatives to equal-rates cladogenesis, it is always wise to compare several different statistics. It is unrealistic to expect any single statistic to be maximally powerful in all scenarios involving differential diversification rates (Chan & Moore, 2002). All statistics have their advantages and disadvantages. Both the temporal and topological methods used here are sensitive to incomplete and/or non-random taxon sampling for the simple reason that these methods do not discriminate between species that have been omitted from a phylogenetic analysis and those that have been eliminated by extinction (Moore & al., 2004). Sampling is incomplete in this study and it has probably not been random (e.g. sampling mainly depended on the availability of silica dried material). Unluckily, this bias is not easy corrected for and results should be interpreted with care, re-running analyses when a more complete sampling is reached. However, the temporal method does not necessarily require a complete sampling as long as the number of taxa within each clade is known. An improvement might be to estimate the phylogenetic position of all unsampled taxa and add their species-richness to the clades to which they probably belong.

In contrast, the balance of a tree can be influenced by omission of even small genera because in that way a complete place-holder taxon is missing. This is important because it has been shown that large phylogenies, from which smaller subclades are omitted, can produce more balanced incomplete trees (Fusco & Cronck, 1995).

Another improvement might be to build a phylogenetic model to explain the genus level diversification rates in Annonaceae, as was done for birds (Phillimore & al., 2006). By using techniques to accommodate phylogenetic labile traits and including a number of ecological variables it was possible to explain more than 50% of the observed variation in diversification rates among families of birds. This is much higher than the previous reported models, where usually only 10-25% of the variation was explained.

CONCLUSIONS

All reconstructed shifts in diversification rate occur in strongly supported parts of the Annonaceae phylogeny, rejecting phylogenetic inaccuracy as an explanation for their origin. It is clear that (except for *Goniothalamus*) the largest genera in the family are not the result of radiations. Also the difference in species numbers between the LBC and SBC cannot be attributed to significant differences in diversification rate along the stem branches of these clades. In general, most of the speciation within Annonaceae was not discernible from a stochastic ERM branching model (i.e. chance). Annonaceae are another example that it is very difficult to explain the variation in clade richness in other terms than stochasticity. This means that no special explanations are necessary for the distribution of species-richness across the major part of Annonaceae phylogeny. It has already been suggested that moderately low rates of dispersal (low enough to interrupt gene flow, but high enough to allow the occasional colonization of new habitats) can result in the highest rates of speciation (Givnish & Systma, 1997) and lead to large clade sizes. Because of the geographic structure in the Short Branch Clade, some clades might be species-rich as the result of a radiation after a founder event. If this indeed was the origin for the species-richness pattern observed here, should be further investigated.

Furthermore, large clade sizes within Annonaceae need not have resulted from intrinsic key-innovations that have influenced the rate of diversification. Only for some clades (e.g. Clade A or *Stenanona*) key-innovations might be invoked to explain the elevated rate of diversification. However, convincingly accepting or ruling out of key-innovations as an explanation would require more formal reconstructions of character evolution, the assessment of many more characters and of course a completer species level phylogeny of Annonaceae.

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SPECIES-RICHNESS DATA

Species numbers for genera were taken from recent Annonaceae literature. Exact estimates of species richness are difficult to obtain due to ongoing taxonomic work. Despite this degree of uncertainty, relative clade sizes are likely to remain similar.

Genus:	**Species estimate:**	**Source genus size:**
Alphonsea	25	Keßler, 1996
Ambavia	2	Morawetz & Le Thomas, 1988
Anaxagorea	26	Scharaschkin & Doyle, 2005
Annickia	8	Versteegh & Sosef, in press
Annona	152	Rainer, 1997; Rainer, 2002; Rainer, pers. comm. 2006
Anonidium	5	Verdcourt, 1971
Artabotrys	100	Verdcourt 1971
Asimina	8	Kral, 1960
Bocageopsis	4	Maas & Westra, in prep.
Cananga	2	Verdcourt, 1971
Cleistopholis	4	Verdcourt, 1971
Craibella	1	Saunders & al., 2004
Cremastosperma	30	Pirie & al., 2005 & 1 undescribed species from CR (M. Pirie, pers. comm. 2006)
Cyathocalyx	36	Wang and Saunders, 2005
Cyathostemma	10	Utteridge, 2000
Cymbopetalum	27	Murray, 1993

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Dasymaschalon	15	Wang, 2006 (pers. comm.)
Desmopsis	18	Schatz, 1987; Maas & al., 1994; Erkens & al., 2006; Schatz, pers. comm. 2006
Diclinanona	3	Maas & al., 1994
Disepalum	9	Johnson, 1989
Duguetia	95	Maas & al., 2003
Enicosanthum	16	Keßler, 1993; Bakker, 2000
Ephedranthus	7	Maas & al., 1994; Chatrou & Pirie, 2003
Fissistigma	60	Tsiang and Li, 1965; Tsiang & al., 1979; Bakker, 2000
Fitzalania	1	Mols, 2004
Friesodielsia	60	Verdcourt, 1971
Fusaea	2	Chatrou and He, 1999
Goniothalamus	120	Saunders, 2003
Greenwayodendron	2	Verdcourt, 1969
Guamia (= Meiogyne)	2	van Heusden, 1994b
Guatteria	280	Maas & al., 1994; Scharf & al., 2005; Scharf & al., 2006; Erkens & al., 2006
Guatteriella (=*Guatteria*)	2	Erkens, in prep.
Guatteriopsis (=*Guatteria*)	5	Erkens, in prep.
Haplostichanthus	6	van Heusden, 1994a
Heteropetalum(=*Guatteria*)	2	Erkens, in prep.
Hornschugia	10	Johnson & Murray, 1995
Isolona	21	Couvreur & al.,
Klarobelia	12	Chatrou, 1998; Chatrou & Pirie, 2003,, 2005
Letestudoxa	3	Chatrou, 1998
Malmea	6	Chatrou, 1998
Marsypopetalum	1	Scheffer, 1870
Meiogyne	14	van Heusden, 1994b; van Heusden, 1996; Schatz, pers. comm. 2006
Melodorum	4	Verdcourt 1971
Mezzettia	4	van der Heijden & Keßler, 1990
Mezzettiopsis (=*Orophea*)	2	Léonardia & Keßler, 2001
Miliusa	25	Mols & Keßler, 2003
Mitrella (= *Fissistigma*, according to Fries, 1959)	5	Sinclair, 1955
Mitrephora	8	Weerasooriya, 2001
Mkilua	1	Verdcourt, 1970; Johnson & Murray, 1995
Monanthotaxis	56	Verdcourt, 1971
Monocarpia	4	Mols & Keßler, 2000a
Monodora	14	Couvreur & al.,
Mosannona	14	Chatrou, 1998
Neostenanthera	4	Aubréville 1969
Neo-uvaria	3	Bakker, 2000
Onychopetalum	2	Maas and Westra, in prep.
Orophea	50	Léonardia & Keßler, 2001; Keßler, 1988; Keßler, 1990
Oxandra	30	Maas & al., 1994; Junikka, 2006 (pers. comm.)
Petalolophus (=*Pseuduvaria*)	1	Su & al., 2005
Phaeanthus	8	Mols & Keßler, 2000b
Piptostigma	14	Hutchinson & Dalziel, 1954; Aubréville 1969
Platymitra	2	Keßler, 1988
Polyalthia	115*	Keßler, 1993; Mols, 2006 (pers. comm.)
Polyalthia hypoleuca complex	6*	Rogstad, 1989; Mols, 2006
Popowia	30	Keßler, 1989
Porcelia	7	Murray, 1993
Pseudartabotrys	1	Chatrou, 1998
Pseudephedranthus	1	Maas & al., 1994
Pseudomalmea	4	Erkens & al., 2006
Pseudoxandra	22	Maas & Westra, 2003; Maas & Westra, 2005
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Pseuduvaria	51	Su, 2002
Rollinia	44	Maas & Westra, 1992
Ruizodendron	1	Maas & al., 1994
Sageraea	9	van Heusden, 1997a
Sapranthus	7	Schatz, 1987
Stelochocarpus	2	van Heusden, 1995
Stenanona	13	Schatz, 1987; Schatz, pers. comm. 2006
Tetrameranthus	6	Westra, 1985
Tridimeris	4	Schatz, 1987; Schatz, pers. comm. 2006
Trigynaea	5	Johnson and Murray, 1995
Trivalvaria	4	van Heusden, 1997b
Unonopsis	45	Maas and Westra, in prep.
Uvaria	150	Meade, 2000
Woodiellantha	1	Rauschert, 1982
Xylopia	145	Johnson, pers. comm. 2006

* *Polyalthia* contains approximately 121 species (Keßler, 2006; Mols, 2006 (pers. comm.)). Phylogenetic studies have shown that it is polyphyletic. The genus is badly in need of revision. The *Polyalthia hypoleuca* complex is being described as a new genus (Mols, in prep.) and is known to contain 6 species. The African and Madagascar *Polyalthia* clade sister to *Miliusa* is estimated at c. 15 species and the *Polyalthia* clade sister to *Marsypopetalum* at c. 5. The remainder of the species is equally distributed over the remaining clades due to the unavailability of a trustworthy estimate of species numbers per clade.

SPECIES-RICHNESS REFERENCES

Bakker, M. E. 2000. *Annonaceae genera worldwide*. ETI, Amsterdam.

Chatrou, L. W. 1998. *Changing genera: Systematic studies in Neotropical and West African Annonaceae.* PhD-thesis. Utrecht University, Utrecht, The Netherlands.

Chatrou, L. W. & He, P. 1999. Studies in Annonaceae XXXIII. A revision of *Fusaea* (Baill.) Saff. *Brittonia* 51: 181-203.

Chatrou, L. W. & Pirie, M. D. 2003. Two new species of Annonaceae from Bolivia. *Rev. Soc. Bol. Bot.* 4: 25-30.

Chatrou, L. W. & Pirie, M. D. 2005. Three new rarely collected or endangered species of Annonaceae from Venezuela. *Blumea* 50: 33-40.

Couvreur, T. L. P., Gereau, R. E., Wieringa, J. J. & Richardson, J. E. In press. Description of four new species of *Monodora* and *Isolona* (Annonaceae) from Tanzania and an overview of Tanzanian Annonaceae diversity. *Adansonia*.

Erkens, R. H. J., Maas, P. J. M., Chatrou, L. W., Schatz, G. E. & Zamora, N. 2006. Seven taxonomic discoveries in Annonaceae from southeastern Central America. *Blumea* 51: 199-220.

Heijden, E. van der & Keßler, P. J. A. 1990. Studies on the tribe Saccopetaleae (Annonaceae) III. Revision of the genus *Mezzettia* Beccari. *Blumea* 35: 217-228.

Heusden, E. C. H. van 1994a. Revision of *Haplostichanthus* (Annonaceae). *Blumea* 39: 215-234.

Heusden, E. C. H. van 1994b. Revision of *Meiogyne* (Annonaceae). *Blumea* 38: 487-511.

Heusden, E. C. H. van 1995. Revision of the southeast Asian genus *Stelechocarpus* (Annonaceae). *Blumea* 40: 429-438.

Heusden, E. C. H. van 1996. The genus *Meiogyne* (Annonaceae) in New Caledonia: four new combinations. *Adansonia* 1-2: 75-83.

Heusden, E. C. H. van 1997a. Revision of the southeast Asian genus *Trivalvaria* (Annonaceae). *Nordic Journal of Botany* 17: 169-180.

Heusden, E. C. H. van 1997b. Revision of the southeast Asian genus *Sageraea* (Annonaceae). *Nordic Journal of Botany* 17: 39-54.

Hutchinson, J. & Dalziel, J. M. 1954. Annonaceae. Pp. 34-54 in, *Flora of West Tropical Africa*, Crown Agents for Oversea Governments and Administrations, London.

Johnson, D. M. 1989. Revision of *Disepalum* (Annonaceae). *Brittonia* 41: 356-378.

Johnson, D. M. & Murray, N. A. 1995. Synopsis of the tribe Bocageeae (Annonaceae), with revisions of *Cardiopetalum, Froesiodendron, Trigynaea, Bocagea*, and *Hornschuchia*. *Brittonia* 47: 248-319.

Keßler, P. J. A. 1988. Studies on the tribe Saccopetaleae (Annonaceae) I. Revision of the genus *Platymitra* Boerlage. *Blumea* 33.

Keßler, P. J. A. 1989. Some notes on different genera of Annonaceae in Malesia. *Annonaceae Newsletter* 7: 1-5.

Keßler, P. J. A. 1990. Studies on the tribe Saccopetaleae (Annonaceae) II. Additions to the genus *Orophea* Blume. *Blumea* 34: 505-516.

Keßler, P. J. A. 1993. Annonaceae. Pp. 93-129 in: Kubitzki, K., Rohwer, J. G. & Bittrich, V., (Eds.), *The families and genera of vascular plants. II Flowering plants - Dicotyledons*, Springer-Verlag, Berlin, Heidelberg, New York.

Keßler, P. J. A. 1996. Studies on the tribe Saccopetaleae (Annonaceae) IV. Revision of the genus *Alphonsea* Hook.f. & Thomson. *Bot. Jahrb. Syst.*118: 81-112.

Kral, R. 1960. A revision of *Asimina* and *Deeringothamnus*. *Brittonia* 12: 233-278.

Léonardia, A. A. P. & Keßler, P. J. A. 2001. Additions to *Orophea* subgenus Sphaerocarpon (Annonaceae): Revision and transfer of *Mezzettiopsis*. *Blumea* 46: 141-163.

Maas, P. J. M. & Westra, L. Y. T. 1992. *Flora Neotropica Monograph 57: Rollinia (Annonaceae)*. The New York Botanical Garden, New York.

Maas, P. J. M., Mennega, E. A. & Westra, L. Y. T. 1994. Studies in Annonaceae XXI. Index to species and intraspecific taxa of neotropical Annonaceae. *Candollea* 49: 389-481.

Maas, P. J. M. & Westra, L. Y. T. 2003. Revision of the Neotropical genus *Pseudoxandra* (Annonaceae). *Blumea* 48: 201-259.

Maas, P. J. M., Westra, L. Y. T. & Chatrou, L. W. 2003. *Flora Neotropica Monograph 88: Duguetia*. The New York Botanical Garden, New York.

Maas, P. J. M. & Westra, L. Y. T. 2005. A new species of *Pseudoxandra* (Annonaceae). *Blumea* 50: 61-64.

Maas, P. J. M. & Westra, L. Y. T. In prep. Revision of *Unonopsis*, *Bocageopsis* and *Onychopetalum*.

Meade, C. V. 2000. *A systematic revision of the Uvaria L. group (Annonaceae) in continental Asia*. PhD-thesis. University of Dublin, Trinity College, Dublin, Ireland.

Mols, J. B. & Keßler, P. J. A. 2000a. Revision of the genus *Phaeanthus* (Annonaceae). *Blumea* 45: 205-233.

Mols, J. B. & Keßler, P. J. A. 2000b. The genus *Monocarpia* (Annonaceae) in Borneo, including a new species *Monocarpia borneensis*. *Bot. Jahrb. Syst.* 122: 233-240.

Mols, J. B. & Keßler, P. J. A. 2003. The genus *Miliusa* (Annonaceae) in the Austro-Malesian area. *Blumea* 48: 421-462.

Mols, J. B. 2004. Identifying clades in Asian Annonaceae: monophyletic genera in the polyphyletic Miliuseae. *Amer. J. Bot.* 91: 590-600.

Morawetz, W. & Le Thomas, A. 1988. Karyology and systematics of the genus *Ambavia* and other Annonaceae from Madagascar. *Plant Syst. Evol.* 158: 155-160.

Murray, N. A. 1993. Revision of *Cymbopetalum* and *Porcelia* (Annonaceae). *Syst. Bot. Mon.* 40: 1-121.

Pirie, M. D., Kankainen, S. & Maas, P. J. M. 2005. *Cremastosperma (and other evolutionary digressions). Molecular phylogenetic, biogeographic, and taxonomic studies in Neotropical Annonaceae*. PhD-thesis. Utrecht University, Utrecht, The Netherlands.

Rainer, H. 1997. Revision of *Annona*, preliminary results and subgeneric grouping. *Annonaceae Newsletter* 11: 44-50.

Rainer, H. 2002. A new species of *Annona* (Annonaceae) from the northeastern Guayana Shield. *Brittonia* 54: 136-140.

Rauschert, S. 1982. Nomina nova generica et combinationes nova Spermatophytorum et Pteridophytorum. *Taxon* 31: 555.

Rogstad, S. H. 1989. The biosystematics and evolution of the *Polyalthia hypoleuca* complex (Annonaceae) of Malesia, I. Systematic treatment. *Journal of the Arnold Arboretum* 70: 153-246.

Saunders, R. M. K. 2003. A synopsis of *Goniothalamus* species (Annonaceae) in Peninsular Malaysia, with a discription of a new species. *Bot. J. Lin. Soc.* 142: 321-339.

Saunders, R. M. K., Su, Y. C. F. & Chalermglin, P. 2004. *Craibella phuyensis* (Annonaceae): A new genus and species from Thailand. *Syst. Bot.* 29: 42-49.

Scharaschkin, T. & Doyle, J. A. 2005. Phylogeny and historical biogeography of *Anaxagorea* (Annonaceae) using morphology and non-coding chloroplast sequence data. *Syst. Bot.* 30: 712-735.

Scharf, U., Maas, P. J. M. & Morawetz, W. 2005. Five new species of *Guatteria* (Annonaceae) from the Pakaraima mountains *Blumea* 50: 563-573.

Scharf, U., Maas, P. J. M. & Morawetz, W. 2006. Five new species of *Guatteria* (Annonaceae) from French Guiana, Guyana and Suriname. *Blumea* 51: 117-130.

Schatz, G. E. 1987. *Systematic and ecological studies in Central American Annonaceae*. PhD-thesis. University of Wisconsin, Madison.

Scheffer, R. H. C. C. 1870. Observationes phytographicae. *Natuurk. Tijdsch. Ned.-Ind.* 31: 338-344.

Sinclair, J. 1955. A revision of the Malayan Annonaceae. *Gard. Bull. Straits Settlem., ser. 3,* 14: 149-516.

Su, Y. C. F. 2002. *Systematics and phylogeny of Pseuduvaria (Annonaceae)*. PhD-thesis. University of Hong Kong, Hong Kong, China.

Su, Y. C. F., Mols, J. B., Takeuchi, W., Keßler, P. J. A. & Saunders, R. M. K. 2005. Reassessing the generic status of *Petalolophus* (Annonaceae): evidence for the evolution of a distinct sapromyophilous lineage within *Pseuduvaria Syst. Bot.* 30: 494-502.

Tsiang, Y. & Li, P.-T. 1965. Revisio specierum sinensium *Fissistigmatis* Griffith. *Acta Phytotax. Sin.* 10: 315-328.

Tsiang, Y., Li, P.-T. & Li, Y.-H. 1979. Angiospermae. Dicotyledonae: Calycanthaceae, Annonaceae, Myristicaceae. Pp. 10-175 in: Tsiang, Y. & Li, P.-T., (Eds.), *Flora Reipublicae Popularis Sinicae*, vol. 30 (2). Academia Sinicae, Peking.

Utteridge, T. M. A. 2000. Revision of the genus *Cyathostemma* (Annonaceae). *Blumea* 45: 377-396.

Verdcourt, B. 1969. The status of the genus *Polyalthia* Blume (Annonaceae) in Africa. *Adansonia* 9: 87-94.

Verdcourt, B. 1970. A new genus of Annonaceae from the East African coastal forests. *Kew Bull.* 24: 449-453.

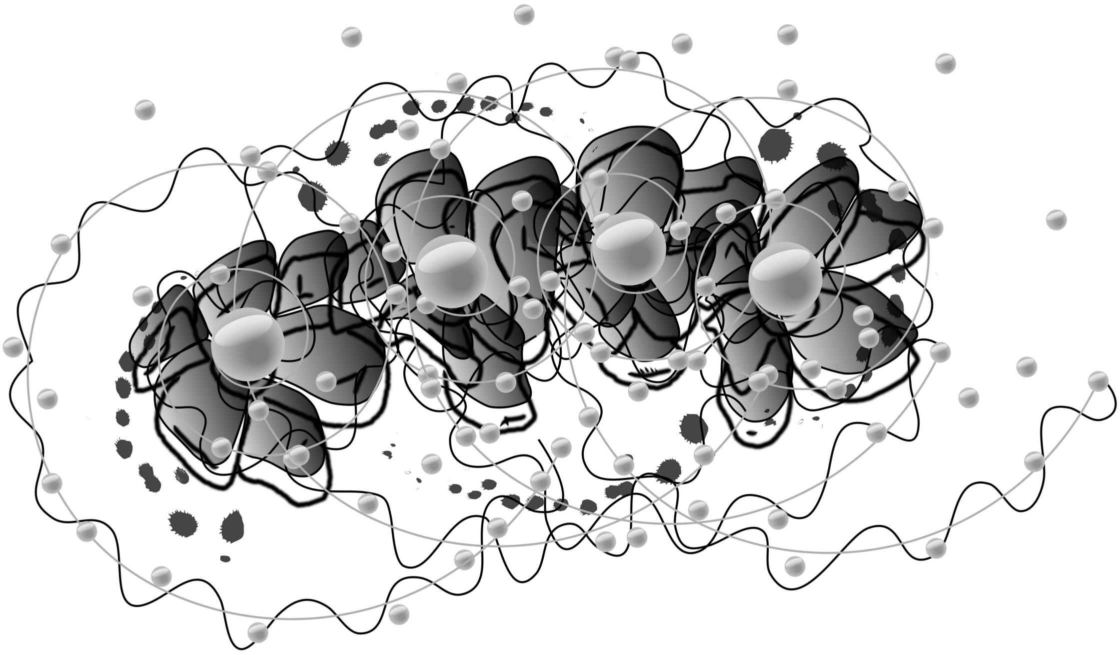
Verdcourt, B. 1971. Annonaceae. Pp. 132 in: Milne-Redhead, E. & Polhill, R. M., (Eds.), *Flora of Tropical East Africa*, Crown Agents for Oversea Governments and Administrations, London.

Versteegh, C. P. C. & Sosef, M. S. M. In press. Revision of the African genus *Annickia* (Annonaceae). *Plant Syst. Geogr.*

Wang, R. J. & Saunders, R. M. K. 2005. The genus *Cyathocalyx* (Annonaceae) in the Philippines. *Syst. Bot.* 31: 285-297.

Weerasooriya, A. D. 2001. *Systematics, phylogeny and reproductive biology of Mitrephora (Annonaceae)*. PhD-thesis. University of Hong Kong, Hong Kong, China.

Westra, L. Y. T. 1985. Studies in Annonaceae IV. A taxonomic revision of *Tetrameranthus* R.E.Fries. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen* C 88: 457-464.



4 A MAJOR RADIATION OF RAINFOREST TREES (*GUATTERIA*; ANNONACEAE) FOLLOWING DISPERSAL FROM CENTRAL INTO SOUTH AMERICA

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ABSTRACT

Several recent studies have suggested that a substantial portion of today's plant diversity in the Neotropics has resulted from the dispersal of taxa into that region rather than vicariance, but more data are needed to substantiate this claim. *Guatteria* (Annonaceae) is, with 265 species, the third largest genus of Neotropical trees after *Inga* (Fabaceae) and *Ocotea* (Lauraceae), and its widespread distribution and frequent occurrence makes the genus an excellent model taxon to study diversification patterns. This study reconstructed the phylogeny of *Guatteria* and inferred three major biogeographical events in the history of this genus: 1) A trans-oceanic Miocene migration from Central into South America before the closing of the Isthmus of Panama; 2) a major diversification of the lineage within South America; and 3) several migrations of South American lineages back into Central America via the closed Panamanian land bridge. Therefore, *Guatteria* is not an Amazonian centred-genus sensu Gentry but a major Miocene radiation that followed its dispersal into South America. This study provides further evidence that migration into the Neotropics was an important factor in the historical assembly of its biodiversity. Furthermore, it is shown that phylogenetic patterns are comparable to those found in *Ocotea* and *Inga* and that a closer comparison of these genera is desirable.

Keywords: radiation, dispersal, Neotropics, rainforest trees, Guatteria, Annonaceae

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INTRODUCTION

The Neotropics hold 30% of the world's plant diversity (Smith & al., 2004) but the origin of this diversity is still debated. Although this immense biodiversity could have arisen in situ, recent studies have suggested that immigration of taxa into South America in the Oligocene and Miocene may have contributed substantially to plant diversity on this continent (Chanderbali & al., 2001; Renner & Meyer, 2001; Davis & al., 2002; Pennington & Dick, 2004; Richardson & al., 2004; Nathan, 2006; Pirie & al., 2006). Molecular phylogenetic studies on the history of species-rich plant genera can contribute to our knowledge of speciation processes, key innovations, and biogeographic patterns. Such genera (e.g. the legume genus *Inga*, c. 300 species or *Eschweilera* (Lecythidaceae), c. 100 species), form a substantial component of the woody element in neotropical forests (in terms of biomass and species numbers) and contribute in an important way to the extraordinary biomass and species diversity in South America (Oliveira & Mori, 1999; Richardson & al., 2001a).

The genus *Guatteria* (Annonaceae) is, with approximately 265 species, one of the largest genera of Neotropical trees along with *Inga* and *Ocotea* (Lauraceae, c. 300 species; (Madriñán, 2004). Species of *Guatteria* are frequent constituents of Neotropical (lowland) forests (Morawetz & Waha, 1985) and the genus is widely distributed throughout Mesoamerica (c. 30 species), the Caribbean (2 species) and South America (c. 230 species). Its widespread distribution and frequent occurrence make the genus an excellent model taxon to study diversification.

Although *Guatteria* is the largest genus in Annonaceae, it can be seen as conservative with regard to its morphological evolution, especially when considering the wide range of morphological differentiation in other large genera of Annonaceae (e.g. *Annona, Uvaria*). Several plant features, such as floral and fruit type, pollen morphology, and chromosome number, are invariable. However, the genus does show a wide ecological distribution and can for instance be found in Amazonian *terra firme* forests, in *campina* types and inundated forests, in Atlantic rain forests, gallery forests, and semidecidious forests (Morawetz & Waha, 1985)., It has therefore been suggested that the main cause of speciation could have been adaptation to a number of different ecological niches in the humid tropics by changes in vegetative characters such as growth form, height, leaf shape and size (Morawetz & Waha, 1985).

Morawetz and Waha (1985) generated the first biogeographic speciation hypothesis for the evolution of *Guatteria*. They suggested that the speciation centre of *Guatteria* could be found in the Amazon basin since the highest species diversity in the genus is there. This distribution pattern can be seen for other taxa as well and the term "Amazonian-centred taxon" was proposed by Gentry to account for this pattern (in contrast to extra-Amazonian, or Andean-centred, taxa; Gentry, 1982). The high species diversity in the Amazon basin is not surprising. The basin has differences in relief, soils, precipitation and seasonality, all leading to a fragmented landscape (Colinvaux, 1996). Furthermore, the dissections of the great river system provide barriers to dispersal (Colinvaux, 1996) and together these factors provide opportunities for allopatric speciation.

The term "Amazonian-centred taxon" could imply that a clade originated and produced the bulk of its species in the Amazonian basin and subsequently dispersed throughout the rest of South and Central America. The idea that a taxon has originated at its point of highest diversity was first suggested by Vavilov (1935) and has been criticised since (reviewed in: Posadas & al., 2006). "Amazonian-centred taxon" could also mean that the Amazon basin functioned as a hotspot for speciation due to the fact that it is a dynamic and fragmented area but that the geographic origin of the genus might be found somewhere else. In the latter case, migration into the Amazon basin led to new opportunities for the evolving taxon, and possibly to a radiation of species.

The aims of this paper are to assess the evolutionary relationships between the major clades of *Guatteria*, to date their origin, test whether *Guatteria* indeed is an Amazonian-centred genus *sensu* Gentry (i.e. it both originated and diversified within the Amazon basin), and finally to gain insight into the causes of speciation.

MATERIALS AND METHODS

Taxon sampling strategy

Species of *Guatteria* were sampled throughout the geographic range of the genus. Furthermore, all major clades in the family as found by Richardson & al. (2004) are included in the analyses, as well as a representative of the sister family of the Annonaceae (Eupomatiaceae; *Eupomatia bennettii*). *Magnolia kobus* was selected as outgroup.
A preliminary analysis of 106 *Guatteria* accessions and based on four plastid regions (*matK*, *rbcL*, *trnL-trnF* and *psbA-trnH*) yielded many most parsimonious trees, and support for individual clades was generally low. Representatives of the larger putative clades from this preliminary analysis were included in matrix A (43 *Guatteria* accessions; voucher information in appendix 1) and sequenced for an additional chloroplast region (*trnT-L*). Matrix A thus contains a limited number of *Guatteria* species but sequence data from five plastid markers. The strict consensus tree resulting from phylogenetic analysis of matrix A was then used as a backbone constraint on the before mentioned larger matrix (matrix B; voucher information in appendix 1), with 106 species but only four plastid regions.

DNA extraction and sequencing

Total genomic DNA from silica-dried leaves and herbarium specimens was extracted from 121 specimens using a modified CTAB method (Doyle & Doyle, 1987). The *matK* gene was amplified and sequenced using primers 390F and 1326R (Cuénoud & al., 2002) and MintF and MintR (Pirie & al., 2005b). Where the 390F primer failed to amplify, the forward primer 390F-2 was used instead (5'-CGYYCATCTGGAAATCTTGGTTC-3'). For *rbcL,* the primers 1F/724R (Olmstead & al., 1992), 636F/1460R (Fay & al., 1997; Fay & al., 1998) and 217F, 922F, 536R and 1104R (Pirie & al., 2005b) were used. The *trnT-trnF* region was amplified and sequenced using primers a, b, c, d, e and f (Taberlet & al., 1991). If problems occurred with the amplification of the *trnT-trnL* spacer the a2 primer designed by Cronn & al. (2002) was used as well. Finally, the *psbA-trnH* intergenic spacer was amplified and sequenced with primers psbA and trnH from Hamilton (1999).

A standard PCR protocol (35 cycles; 30 sec.: 94°C; 30 sec.: 53°C; 1 min.: 72°C; with an initial 5 min.: 94°C and final 10 min.: 72°C) was used and 0.4% BSA was added to the mixes. PCR products were purified using the QIAquick PCR purification kit (Qiagen) and cycle-sequenced with DYE-ET terminators (Amersham) and run on an ABI 3730XL automated DNA sequencer.

Phylogenetic analyses

Sequences were edited and assembled in SeqMan 4.0 (DNAStar Inc., Madison, WI), alignment was done by eye and simple indel coding (Simmons & Ochoterena, 2000) was applied. Most-parsimonious trees were generated from 10,000 replicates of random taxon addition and swapped using tree bisection-reconnection (TBR), equal weights and a maximum of five trees held at each step, using PAUP* 4.0b10 (Swofford, 2003). Bootstrap analysis (Felsenstein, 1985) of 10,000 replicates with "full" heuristic searches of 10 random addition sequences was performed, equal weights and TBR swapping, saving a maximum of 5 trees at each replicate. Bootstrap support of 50–74% is considered to represent weak support, 75–89% moderate support and 90–100% strong support. The strict consensus from the analysis of matrix A was used as a backbone constraint on matrix B. The search for most parsimonious trees was repeated as described above, as well as the bootstrap analysis.

The data were also analysed with Bayesian inference using MrBayes version 3.1.1 (Huelsenbeck & Ronquist, 2001); analyses were run for 5,000,000 generations with six simultaneous Monte Carlo Markov Chains, and one tree sampled per 100 generations. Parameters for the general model of DNA substitution (GTR with gamma-distributed rate variation across sites) for the separate partitions were estimated by MrBayes. All partitions were allowed to have their unique model and the overall evolutionary rate was allowed to be (potentially) different across partitions. Only parsimony informative characters were coded as indels and MrBayes was informed of this coding bias in order to calculate the probability of the data correctly (using the "lset coding=informative" option).

Age estimation

Maximum likelihood as implemented in PAUP* was used to calculate branch lengths from both matrices with the DNA substitution models that were indicated as optimal for the combined data partitions of matrix A (TIM + I + G) and matrix B (TVM + I + G) by Modeltest v. 3.06 (Posada & Crandall, 1998). Both matrices were used to estimate ages of clades so that these ages could be compared between data sets. Rate heterogeneity among lineages was evaluated using the likelihood ratio test (Felsenstein, 1988). For both matrices a molecular clock was rejected because the log likelihoods of the unconstrained and constrained analyses were significantly different (matrix A: 19,363.05 versus 21,813.6, $P<0.001$; matrix B: 16,135.65 versus 16,331.93, $P<0.001$). Therefore, non parametric rate smoothing (NPRS; Sanderson, 1997) and penalized likelihood (PL; Sanderson, 2002) were used to estimate divergence times, using the software package r8s (Sanderson, 2004).

Three calibration points were used in this study: (1) the age estimate by Wikström & al. (2001) for the stem of Annonaceae (figure 1, marked "Wi"; 82 my), (2) fossil seeds from the Maastrichtian in Nigeria, well-characterised with their lamelliform ruminations (Chesters, 1955); figure 1, marked "Fo"; 68 my), and (3) the endemic occurrence of *Guatteria caribaea* on the Lesser Antilles (Puerto Rico, Guadeloupe, Dominica, Martinique, Saint Lucia and Nevis; (Fries, 1939). Although originating from the late Eocene, these islands may not have been permanently uplifted. In their present form the majority of them are younger than the

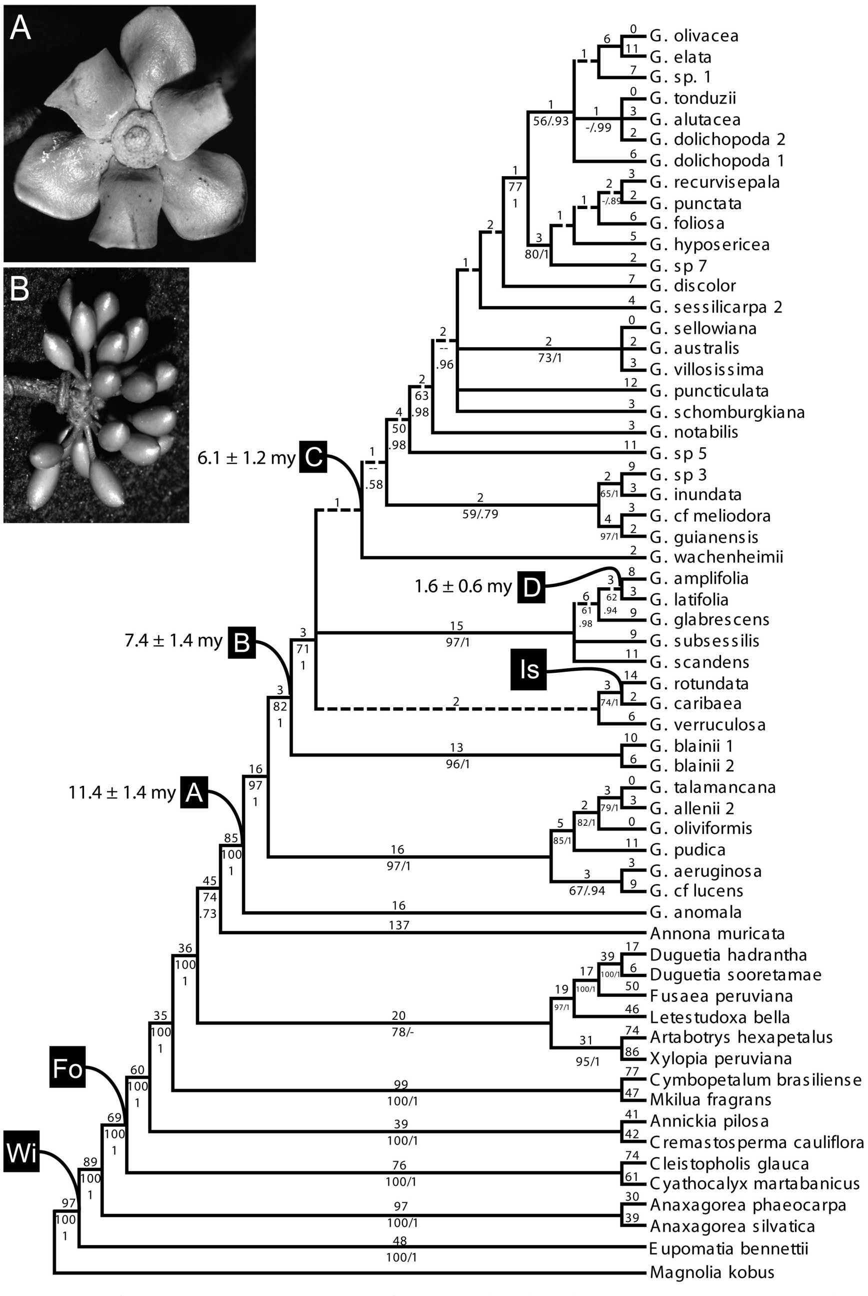

Figure 1. One of 41,968 most parsimonious trees from an analysis based on *matK*, *trnTL*, *trnLF*, *rbcL* and *psbA-trnH* (matrix A). Branch lengths are shown above the branches, bootstrap percentages and Bayesian posterior probabilities below. Branches absent in the strict consensus of all most parsimonious trees are indicated by dashed lines. Calibration points are marked with Wi (Wikström, 82 my), Fo (Maastrichtian seed, 68 my) and Is (maximum age of the Lesser Antilles, 6 my; see text). Dated nodes based upon PL are labelled A-D (node A: 11.4 ± 1.4 my, node B: 7.4 ± 1.4 my, node C: 6.1 ± 1.2 my, node D: 1.6 ± 0.6 my). Photograph A. open flower bud of *Guatteria oliviformis*; B. Fruits of *Guatteria allenii*.

Pliocene (Iturralde-Vinent & MacPhee, 1999). Although objections exist against the use of the age of strata on which endemic taxa occur for calibrating phylogenetic trees (see Heads (2005) for a critique), it is the only additional calibration point possible within *Guatteria* since there are no known fossils. Therefore, the split between *G. caribaea* and *G. rotundata* was constrained to a maximum age of 6 million years (figure 1, marked ″Is″). For a discussion on the placement and accuracy of calibration point (1) and (2) see Richardson & al. (2004). Mean values and confidence intervals for all dates were calculated by reapplying NPRS and PL to 100 bootstrapped matrices (Sanderson, 2004).

Biogeography

Species distributions were scored using floristic regions as described by Takhtajan (Takhtajan, 1986). Within the Neotropical Kingdom he specifies the Caribbean, Guyana Highlands, Amazonian, Brazilian and Andean regions. The occurrences of the different species within these regions were mapped onto the cladogram in figure 2 and optimised over the tree with MacClade version 4.08 (Maddison & Maddison, 2000) using Fitch optimisation (Fitch, 1971).

RESULTS

Phylogeny and geography of speciation

For the 60 accessions in matrix A, the *matK*, *rbcL*, *trnT-trnF* and *psbA-trnH* plastid DNA regions were sequenced, with the exception of *Eupomatia bennettii* for which no *matK*, *psbA-trnH* and *trnTL* sequences were obtained, *Magnolia kobus*, *Guatteria cf. lucens* and *G. blainii* 1 of which the *trnTL* region failed to amplify, and *Cyathocalyx martabanicus* and *Annona muricata* for which only partial *trnTL* could be sequenced. Matrix B contained no missing data, except for the above mentioned outgroup sequences.

Phylogenetic analysis of matrix A resulted in 41,968 most parsimonious trees of 2192 steps, with a consistency index (CI) of 0.78 and retention index (RI) of 0.84. One of the most parsimonious trees is shown in figure 1. The relationships within the outgroup taxa are fully congruent with Richardson & al. (2004) and are in general strongly supported. *Guatteria* proves to be monophyletic, receiving bootstrap support (BS) of 100% and a posterior probability (PP) of 1.0 and is subtended by a relatively long branch of 85 substitutions. Early-diverging relationships within the genus generally have strong support but towards the tips of the tree support values decline.

The strict consensus of the trees from matrix A (figure 1) was used as a backbone constraint on matrix B and subsequent phylogenetic analysis of this matrix resulted in 39,305 most parsimonious trees of 1826 steps (CI 0.72; RI 0.83). One of the most parsimonious trees is shown in figure 2, including optimised geographical areas. Due to the backbone constraint used, relationships within the outgroups receive high bootstrap support (not shown) as

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Figure 2. (next page) One of 39,305 most parsimonious trees from an analysis based on *matK*, *trnLF*, *rbcL* and *psbA-trnH* (matrix B). Branch lengths are shown above the branches, bootstrap percentages and Bayesian posterior probabilities below. Age estimates for nodes are based upon PL analysis of matrix A and are labelled A-D. Optimised geographical areas are indicated at the nodes as CA (Central American) or SA (South American). Geographic distribution of the species is also shown. Solid square boxes indicate species within the ″South American Clade″ that are of Central American distribution. The arrow indicates the possible onset of the radiation. Outgroups were pruned, except for *Annona muricata*. Relationships and support for pruned outgroups are equal to figure 1

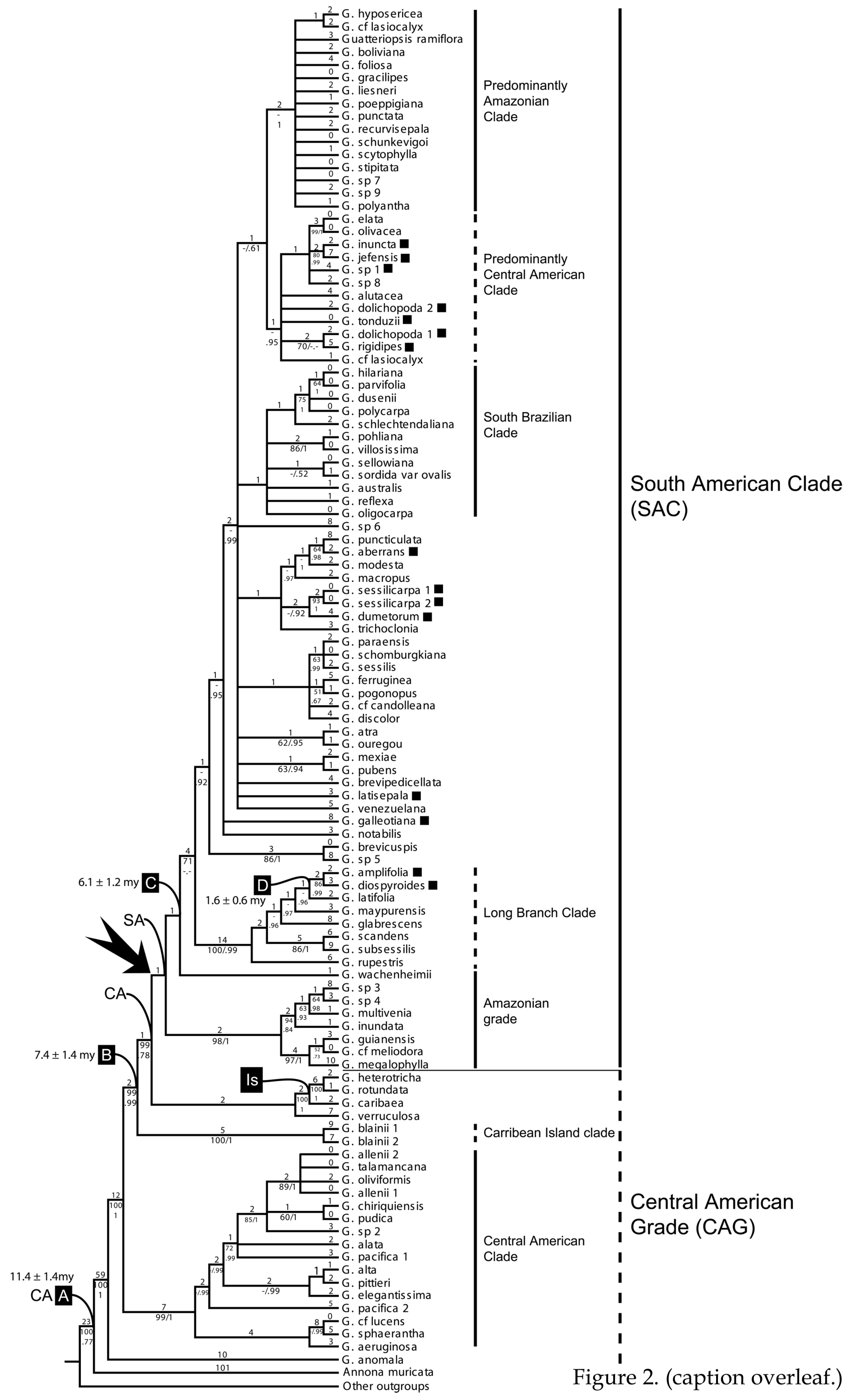

Figure 2. (caption overleaf.)

well as the early diverging relationships within *Guatteria*. However, the unconstrained and independent Bayesian analysis corroborates the result found by the bootstrap analysis. *Guatteria anomala* from Mexico and Guatemala is sister to the rest of the genus and is part of a grade (Central American grade; CAG) consisting of species from Central America, the Caribbean Islands (*G. blainii* and *G. caribaea*) and some species from the west side of the Andes in Colombia. Therefore, the crown node of *Guatteria* resolves as Central American (figure 2, node A). From within this grade a clade is derived in which bootstrap support is in general weak or absent. This clade primarily contains South American species and hence this clade will be referred to as the South American Clade (SAC). The crown node of this clade resolves as South American (figure 2, indicated by SA). In contrast to the bootstrap analysis, the Bayesian yields a better supported backbone topology in the SAC. Generally, both analyses show lack of support for relationships towards the tips of the tree in the SAC. One clade is exceptional with regard to the length of the branch leading to it. The Long Branch Clade containing *G. scandens, G. subsessilis, G. glabrescens, G. latifolia,* and *G. amplifolia* (BS 100% ; PP 0.99) is subtended by a relatively long branch of 14 substitutions, the longest branch within the topology. Lastly, the node connecting the *G. verruculosa* – *G. heterotricha* clade with its sister is reconstructed as Central American (figure 2, indicated by CA).

Timing of diversification

Age estimates on the basis of matrix A were always younger than those based on matrix B. Also, estimates calculated with PL were always younger than those calculated with NPRS (table 1). Regarding variation in substitution rate PL is considered to provide the best estimates for ages because NPRS tends to over-smooth short branches (Sanderson, 1997; 2004) and many short branches are present in the tree in figure 2. Because age estimates must be seen as minimum ages only the youngest age estimates (based on PL and conducted on matrix A) will be reported in the text. The node connecting the *G. caribaea* - *G. rotundata* clade with its sister, *G. verruculosa*, does not have high bootstrap and/or Bayesian support values. It might be argued that this uncertainty in relationships might influence the dating of the tree because the occurrence of *G. caribaea* on the Caribbean islands is used as a calibration point. However, removing this calibration point from the analysis did not result in different age estimates (data not shown).

The crown node of *Guatteria* is dated at least 11.4 ± 1.4 my (figure 1, node A). The node connecting the *G. blainii* clade and the rest of the genus has an estimated age of at least 7.4 ± 1.4 my (figure 1, node B). The age of the node linking *G. wachenheimii* with its sister group was estimated at least 6.1 ± 1.2 my (figure 1, node C). Finally, the split between the Central American species *G. amplifolia* and its South American sister species *G. latifolia* was

Table 1. Mean age estimates with standard deviations (million years) from bootstrap resampled analyses for selected nodes of Guatteria based upon PL and NPRS analyses of matrix A and B. Node B did not occur in the trees from the bootstrap resampling analyses of matrix B. Age constraints for calibration are marked in figure 1 and 2. Nodes are those labelled in figure 1 and 2.

Node	Matrix A,	Matrix A, PL	Matrix B,	Matrix B, PL
A	21.5 ± 1.7	11.4 ± 1.4	29.9 ± 2.1	25.7 ± 5.2
B	16.0 ± 1.8	7.4 ± 1.4	-	-
C	13.1 ± 1.8	6.1 ± 1.2	21.0 ± 2.7	19.5 ± 5.5
D	3.3 ± 1.1	1.6 ± 0.6	5.0 ± 1.7	5.3 ± 2.5

dated at least 1.6 ± 0.6 my (figure 1, node D).

DISCUSSION

Lack of resolution indicates a radiation

Although it was possible to reconstruct the phylogenetic relationships between several clades within *Guatteria*, the majority of the relationships remain unclear. There is a lack of informative characters leading to many short branches and hence low resolution. This pattern is comparable to that found by Richardson & al. (2001) in *Inga*, noteworthy because both genera are comparable in their size and distribution. *Inga* is considered a rapidly diversifying, species rich genus because most estimates place diversification in *Inga* within the last 10 my (with many species arising as recently as 2 million years ago). The crown group of *Guatteria* was estimated to be at least 11.4 ± 1.4 my of age. The minimum age of the SAC, which contains most of the species diversity, is estimated at between 6.1 ± 1.2 and 7.4 ± 1.4 my (figure 1 and 2, node B and C). Thus, for *Guatteria* as well as *Inga* most speciation occurred relatively recent and *Guatteria* might therefore also be called a rapidly diversifying, species-rich genus. The fact that internal branch lengths in the SAC are significantly shorter than in the CAG (t-test, $P<0.05$; matrix A and B) supports the hypothesis that the SAC represents a rapid diversification.

Geography of speciation

Amazonian-centred genera sensu Gentry are autochthonous South American and their main diversity is found in the Amazon (Gentry, 1982). Because *Guatteria* has its highest species diversity there, it could be argued that *Guatteria* is such a genus. Furthermore, most of the Amazonian-centred taxa are canopy trees and lianas and *Guatteria* for 99% comprises trees. Next to this, according to Gentry the Amazonian-centred taxa are poorly represented in Central America with only c. 15% of their species there. *Guatteria* contains only c. 30 Central-American species (c. 12%).

In order to test whether *Guatteria* is Amazonian-centred it is necessary to know where the genus originated and how it spread throughout the Neotropics. Optimisation of geographical distributions onto the tree in figure 2 shows that the crown node of the SAC is optimised as South American, while the more basal nodes are all optimised as Central American. These data suggest that the most recent common ancestor of all extant *Guatteria* species arose in the early Miocene of what now is called Central America (figure 2). The hypothesis that early diversification took place in proto-Central America is further supported by the fact that the basal lineages comprise solely of species from Central America, the Caribbean Islands or species from the west side of the Andes in Colombia. That the SAC is derived from within this clade implies that *Guatteria* dispersed into South America in the late Miocene (figure 2). Because of the timing of this migration *Guatteria* moved into South America before the complete closure of the Isthmus of Panama (c. 3-3.5 my ago) and subsequently diversified rapidly.

The more ancient evolutionary history of the CAG is reflected in the morphology of the species. The species in the CAG are mostly endemic to Central America, a high level of endemism that is expected from the isolation of a landmass for a considerable amount of time (Burnham & Graham, 1999). Morphologically they are easier to distinguish than the species in the large SAC clade. In contrast, the SAC contains many widespread species and species complexes. Several of these species have entered Central America again (figure 2) and are part of morphologically difficult complexes (e.g. *G. dolichopoda*, *G. tonduzii* and *G. rigidipes* or *G. amplifolia* and *G. diospyroides*). Many intermediates are present between the putative Central American and South American species. The closer alliance of the re-migrants to the South American, rather than to the other Central American, *Guatteria* species is corroborated by a seven base pair insertion in the *trnLF* region (the only supporting character on that particular node in figure 2), a synapomorphy for *G. anomala* and all the species in the CAC and the Caribbean clade.

Simpson (1975) generated a list of 14 genera that must have been immigrants to South America from the north (although she was unable to estimate the timing of arrival). She mentions *Bomarea, Ranunculus, Lupinus, Gentiana* and *Senecio* among others. In contrast to *Guatteria* only few of these genera show radiation following their arrival in South America. Central American distributional centres have also been suggested for genera as *Ocotea, Beilschmiedia, Cedrela, Luehea, Oreopanax,* and *Swartzia* on the basis of fossil data (Leopold & MacGinitie, 1972). Especially *Ocotea* (Lauraceae) is interesting in this respect. With c. 300 species (Madriñán, 2004) it is, next to *Guatteria* and *Inga*, one of the largest Neotropical genera that predominantly comprise trees. The fossil record is inadequate to show when the modern distribution was reached but phytogeographic and ecological evidence suggests that it was before the closure of the Panamanian land bridge (Gentry, 1982). This conclusion is supported by phylogenetic analyses that estimate an early Miocene arrival of the *Ocotea* complex in South America (Chanderbali & al., 2001; Renner, 2004). Furthermore, similar to *Guatteria* a Central America-centred species group in *Ocotea* is sister to a South America-centred species rich group and the split between these lineages is estimated at 20 my.

The predicted diversity for a group of plants isolated in South America until the establishment of the Panamanian land bridge would be a high number of species in South America, with only a few, perhaps widespread, taxa extending into Central America. This pattern has indeed been found for many genera (Burnham & Graham, 1999) but cannot be acknowledged for *Guatteria*. Most of the Central American *Guatteria* species are endemic. Only one or two species occur outside Central America (mostly in undercollected regions in Colombia), and just one species (*G. recurvisepala*) is probably widespread with its distribution throughout Central America, Venezuela and the Guianas.

Based on all of the above it can be concluded that *Guatteria* is not an autochthonous South American genus but has dispersed into that region at some time during the Miocene.

Migrations in the evolution of Guatteria

Three events are of particular importance in the history of the South American continent in the last 15-20 my (Gentry, 1982; Burnham & Graham, 1999): 1) the Andean orogony, 2) the closing of the Isthmus of Panama and 3) the Pleistocene climatic fluctuations.

The major period of uplift in northern South America occurred in the Miocene epoch (Burnham & Graham, 1999) and resulted in the formation of the Andes. By the late Miocene epoch the Cordillera Oriental in Colombia is estimated to have reached an altitude of around 1000m (Wijninga, 1996) but most of the uplift took place only in the last 5 my

(Gentry, 1982). The fact that the crown of the SAC is at least 6.1-7.4 my old might mean that migration of *Guatteria* into South America took place before the Andes proved an effective barrier. According to Chanderbali & al. (2001), the timing of the separation between the Central America-centred species group and the South America-centred species rich group in *Ocotea* coincides with increased uplift of the northern Andes in the early Miocene. Therefore they state that it is conceivable that the Andean orogeny divided the ancestral range of *Ocotea.* However, here it is believed that migration across the submerged Panamanian land bridge might have been a more important event in splitting the Central and South American lineages, at least for *Guatteria,* than the relatively low altitude of the Andes in the early Miocene. Nevertheless, the Andes might nowadays be an effective barrier against (re)migration.

Next to Andean orogeny the closing of the Isthmus of Panama was one of the most important events for the Latin American biota because it enabled easy migration between North and South America. The definitive closure of the isthmus has been estimated around 3-3.5 my ago (Coates & Obando, 1996) and is known to have caused the so-called "Great American Interchange" in animals. The land bridge appears to be far less significant in angiosperms and numbers of South American species derived from northern immigrants are estimated at about 10% (Burnham & Graham, 1999). Indeed, in the case of *Guatteria* the submerged land bridge did not seem an obstacle against migration. On the other hand, the estimate of at least 6.1 ± 1.2 my for the migration of *Guatteria* into South America is about the same age as a hypothesised short-lived terrestrial corridor around c. 4-7 my ago (Bermingham & Martin, 1998). In addition, Iturralde-Vinent and MacPhee (1999) suggested a land bridge that could have existed between c. 8.5 and 14 my and Pennington & Dick (2004) put forward even other possibilities for land bridges. Therefore, migration might not have taken place across a large water barrier but via stepping stones.

While the first arrival of *Guatteria* in South America took place prior to the definitive Pliocene closure of the Isthmus, the remigration into Central America could have happened after closure, as for example can be seen from the split between the Central American *G. amplifolia - G. diospyroides* lineage and its South American sister that is estimated at a minimum of 1.6 ± 0.6 my (figure 1 and 2, node D).

The third important event in the history of South America are the Pleistocene climatic fluctuations, associated with glacial advances and retreats at higher altitudes. Data of Pennington & al. (2004) show that Pleistocene diversification plays an important role in Central American semi-deciduous tropical forests. In *Inga* some evidence exist for Pleistocene speciation in Neotropical rain forests (Richardson & al., 2001a). *Guatteria* occurs nearly exclusively in wet evergreen forests and in this study the many recent speciation events seem to suggest that at least some part of the extant diversity in *Guatteria* is due to Pliocene or even Pleistocene speciation. However, the impact of the climatic fluctuations is difficult to assess on the basis of the current data set.

Ecological speciation and vicariance

The link between species proliferation and adaptive diversification in *Guatteria* seems very weak, especially in the SAC. This observation seems to corroborate the suggestion of (Morawetz & Waha, 1985) that the main cause of speciation in *Guatteria* could have been adaptation to a number of different ecological niches by changes in vegetative characters. Phylogenetic analyses by Fine & al. (2005) showed that multiple putative sister taxa with parapatric distributions differ in their edaphic associations, suggesting that edaphic heterogeneity was an important driver of speciation in the tribe Protieae (Burseraceae) in the Amazon basin. A comparable mechanism might also be responsible for speciation in *Guatteria*. Morawetz and Waha (1985) might have been right by pinpointing the Amazon as speciation centre because the basin might have played a pivotal role in the rapid diversification of *Guatteria*. However, the ecological and phylogenetic data needed to test this hypothesis thoroughly is presently lacking.

An alternative explanation for species-richness in *Guatteria* is that its populations might have been subdivided on a regular basis due to abiotic factors. In such a case no one character or set of characters would be causally involved in promoting speciation (Cracraft, 1985). Although support is weak, a few geographically delimited clades can be seen in figure 2, suggesting at least some influence of geography on the origin of lineages. For instance with regard to the predominantly Amazonian or Central American clades, the fragmented landscape of the Amazon basin (Colinvaux, 1996) or the complex geological history of Central America (Iturralde-Vinent, 1999) would have provided ample opportunities for sequences of vicariant events leading to allopatric speciation, though with only negligible adaptive divergence between the vicariant species (Skelton, 1993).

CONCLUSIONS

It seems that the evolutionary history of *Guatteria* can be regarded as a three step process: 1) a trans-oceanic Miocene migration from Central into South America before the closing of the Isthmus of Panama, unhampered by the low altitude of the Andes; 2) a subsequent major diversification of tree species in South America; and 3) several small remigrations of South American lineages into Central America across the Andes and over the closed Panamanian land bridge. We can therefore conclude that *Guatteria* is not an Amazonian centred-genus *sensu* Gentry but a recent major radiation after dispersal into South America. As brought to attention by Pennington & Dick (2004) the contribution of immigrant taxa to the South American rainforest flora needs a re-evaluation in order to properly understand the historical assembly of its biodiversity. *Guatteria* proves the importance of their claim, whilst providing another case in which migration into South America might have contributed substantially to South American speciation. Furthermore, a closer comparison of the evolutionary history of *Ocotea*, *Inga* and *Guatteria* is highly desirable because all three large Neotropical tree genera might show comparable phylogenetic patterns and timings.

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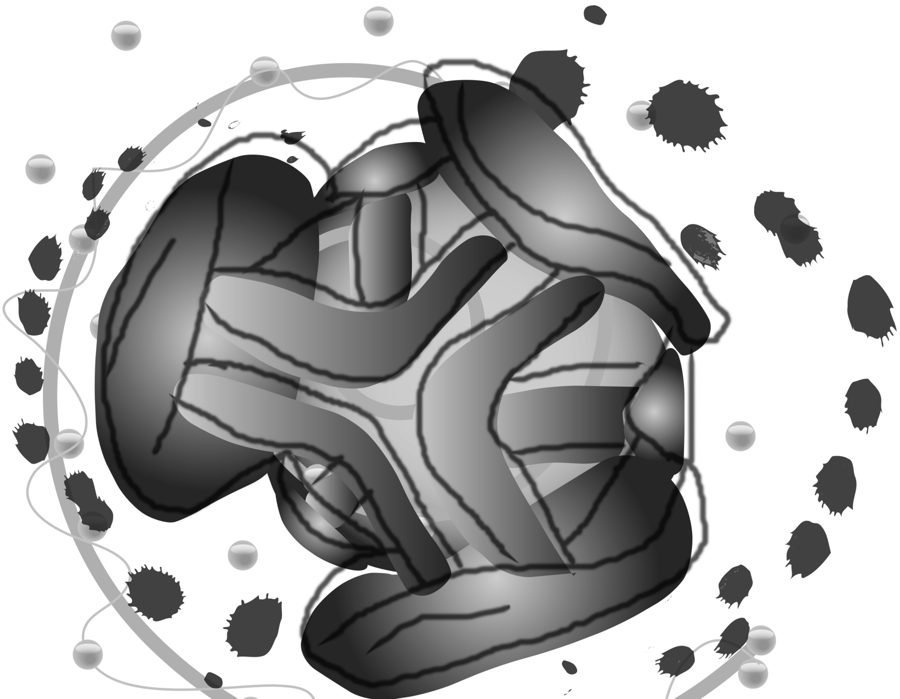

5

EVOLUTION AND CLASSIFICATION OF A LARGE AND WIDESPREAD GENUS OF NEOTROPICAL TREES (*GUATTERIA*; ANNONACEAE) AND ITS THREE SATELLITE GENERA (*GUATTERIELLA*, *GUATTERIOPSIS* AND *HETEROPETALUM*)

Roy H.J. Erkens, Lars W. Chatrou[2], Jifke Koek-Noorman[1], Jan W. Maas[1] & Paul J.M. Maas[1]

ABSTRACT

Species-rich genera potentially provide important cases for the study of speciation processes, key innovations and biogeographic patterns because of their large number of species, ecological importance and widespread distribution. *Guatteria* (Annonaceae) is, with c. 265 species, the third largest genus of Neotropical trees, after *Inga* and *Ocotea*. The use of *Guatteria* as a model in studies on for instance key innovations has so far been severely hampered because of problems concerning taxonomy and classification, caused by the uniform morphology of the genus. This study focuses on the molecular phylogenetic relationships between species of *Guatteria* and species of its three smaller satellite genera (*Guatteriopsis*, *Guatteriella* and *Heteropetalum*), and the implications of these relationships for classification and character evolution. Results show that *Guatteriopsis*, *Guatteriella* and *Heteropetalum* should be submerged into *Guatteria*. *Heteropetalum* could be put into its own subgenus because of its aberrant morphology and *Guatteriopsis* and *Guatteriella* might be given sectional status. With regard to the currently recognised sections it can be concluded that most of them are probably non-monophyletic. However, a completely new subgeneric classification of *Guatteria* would be premature because of the lack of molecular and morphological synapomorphies to define new sections. Lastly, the *Guatteria* archetype as exemplified by the genus description may have evolved only after the divergence of several early branching lineages.

Keywords: molecular phylogenetics, classification, sections, wood anatomy, character evolution

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Taxon, in press

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INTRODUCTION

The evolutionary most successful woody plants, in terms of species richness, can be found amongst tropical trees. Among extant woody plants, several genera of tropical trees show taxonomic diversification beyond comparison. In the tropical areas of the New World, for example, some genera proliferated into very large genera of 200-350 species, as exemplified by *Inga* (Fabaceae, c. 300 spp.; Richardson & al., 2001a) and *Ocotea* (Lauraceae; c. 300 spp.; Madriñán, 2004; but see Rohwer, 2005). The Neotropical genus *Guatteria*, with approximately 265 species, is the largest genus within the family of Annonaceae (Chatrou & al., 2004), and represents approximately 10% of the species diversity within the family. After *Inga* and *Ocotea* it is the third largest genus of Neotropical trees. The genus is distributed throughout Mesoamerica, South America and the Caribbean Islands and occurs mainly in lowland (rain)forests but some species can be found at elevations of over 2000 m in Andean forests.

Because of their large numbers of species, ecological importance, and widespread distribution, these genera potentially provide important cases for the study of speciation processes (e.g., in *Inga*; Richardson & al., 2001a). Also key innovations that promoted diversification and biogeographic patterns can be investigated (e.g., the Ocotea complex; Chanderbali & al., 2001). However, their use in such studies is often impeded because of problems concerning taxonomy and classification. Particularly, these large genera are often notable for their uniformity of morphology. In *Inga*, for example, neither morphology nor anatomy contributes to a clear infrageneric classification (Pennington, 1997). Divisions into sections are highly artificial and section limits are blurred, with intermediates always present between sections.

The infrageneric classification of *Guatteria* is problematic as well. Ruiz and Pavón described the genus as early as 1794 and since then many species have been described but the last and only revision dates back to Fries (1939). At first he recognised 30 sections. Due to the availability of many new collections, infrageneric classification was revised again, and the genus was divided into two subgenera, keeping only 22 of the original sections, some however with new circumscriptions (Fries, 1955a; 1959). Unfortunately, circumscriptions of most sections are based on few macro morphological characters, which often are difficult to interpret, such as shape of the petals, the indument of the prolonged stamen connective, or the shape of the monocarps. For some sections the delimiting characters are not clear at all.

Van Heusden (1992) reports on the very uniform flowers throughout the genus and similar uniformity has been reported on the morphology of fruits, seeds (van Setten & Koek-Noorman, 1992) and leaf anatomy (van Setten & Koek-Noorman, 1986). This homogeneity in morphological characters makes it difficult to understand the systematics and evolution of the genus. The lack of a taxonomic framework in its turn severely hampers the evaluation of the large quantities of new material that have been collected throughout the recent years, and the inclusion of necessary, high quality taxonomic data into local or national floras, and into decision making policies about conservation. Furthermore, it inhibits the search for characters that are phylogenetically informative (Meade & Parnell, 1998). To date, *Guatteria* is the only major genus of Neotropical Annonaceae awaiting revision.

Based on morphological characters, *Guatteria* belongs to Fries' *Guatteria* group (Fries, 1939; 1959), consisting of four genera: *Guatteria* (Fig 1A), *Guatteriopsis* (Fig 1B), *Guatteriella* (Fig 1C), and *Heteropetalum* (Fig 1D). *Guatteria* is easily recognised by a combination of an impressed primary vein on the upper side of the leaf, valvate sepals, almost always imbricate petals, numerous carpels (with a single basal ovule), and a pedicel with a distinct suprabasal articulation. *Guatteriopsis* ("Guatteria-like"; Fries, 1934) is made up of five species (*G. blepharophylla* (Amazonian Brazil, Peru, Guyana, Amazonian Ecuador, and Venezuela), *G. friesiana* (Amazonian Brazil and Amazonian Colombia), *G. hispida* (Amazonian Brazil), *G. kuhlmannii* (Amazonian Brazil), and *G. ramiflora* (Amazonian Peru). It is distinguishable from *Guatteria* by the fact that both whorls of petals are valvate (non-overlapping) instead of imbricate (overlapping). *Guatteriella* ("small Guatteria"; Fries, 1939) consists of only two species (*G. campinensis* (Amazonian Brazil), and *G. tomentosa* (Amazonian Brazil and Amazonian Colombia)). The genus is characterised by laterally flattened, (hairy) monocarps, thick and densely hairy, brownish yellow petals, and a percurrent straight tertiary venation. Fries (1939), and Morawetz and Maas (1984) mention the possible intermediate position of *Guatteriella* between *Guatteria* and *Guatteriopsis*. The fourth genus in the *Guatteria* group is *Heteropetalum* ("unequal petals"; Fries, 1930) made up of two species (*H. brasiliense* and *H. spruceanum*, both from Amazonian Brazil, southern Venezuela and southern Colombia). *Heteropetalum* differs from *Guatteria* because the outer petals are greatly reduced in size (becoming almost sepal-like).

The close affinity between the genera of the *Guatteria* group has been suggested by many authors after Fries (1939; 1943; 1959) on the basis of leaf anatomy (van Setten & Koek-Noorman, 1986), flower anatomy (van Heusden, 1992), fruit and seed morphology (van Setten & Koek-Noorman, 1992), unusual chromosome differentiation and cuticular folding patterns (Morawetz & Waha, 1985), a distinct pollen type (Walker, 1971; Morawetz & Waha, 1985), and oil composition analysis (Maia & al., 2005). This close affinity was corroborated in an unpublished phylogenetic study based on plastid *rbcL* sequences (Bygrave, 2000). However, the exact phylogenetic relationships among these genera have never been established. Next to this, the character states for the above mentioned characters for the *Guatteria* group are unique within the family, causing a systematically somewhat isolated position of the group as a whole. This position is still under debate because a preliminary phylogenetic study of Annonaceae on the basis of seven plastid markers could not unambiguously identify its sistergroup (unpublished data).

The constituent genera of the *Guatteria* group are morphologically highly similar. Nonetheless, because differing by a small number of conspicuous characters, they have been given generic status. At the infrageneric level the nondescript morphology of *Guatteria* is reflected by the fact that some highly uniform groups of species each have been given the status of section. The question is how this can be interpreted in a phylogenetic context. In fact, analyses of phylogenetic relationships among large genera and their putative satellite genera, and among sections within large genera, have been going on, on a large scale over the last years (e.g. Schneeweiss & al., 2004; Schneider & al., 2004; Simões & al., 2004; Wang & al., 2005). These studies allow revising classification, such that only monophyletic groups are recognised and named. Also, appropriate groups are defined for biogeographical analysis or analysis of character evolution, which is important as analysing paraphyletic clades compromises evolutionary integrity (de Queiroz, 1988) and leads to arbitrary results.

The present paper focuses on the phylogenetic relationships within *Guatteria*, and between *Guatteria* and its satellite genera, and implications for classification and character evolution, in particular gross morphology and wood anatomy. This approach allows optimisation of morphological characters onto a phylogeny, and analysis of whether the significant divergence of *Guatteria* is attributable to the origin of some characters. In such a scenario, the satellite genera may have diverged before a typical suite of characters of *Guatteria* canalised. Alternatively, the satellite genera might be nested within *Guatteria*, in which case the small genera represent the origin of some morphological autapomorphies.

MATERIALS AND METHODS

Plant material and taxon selection

This study uses sequence data of 145 Guatteria (figure 1A) accessions obtained from silica dried material or herbarium sheets (voucher information in Appendix 1). Out of 265 species 102 were sampled (c. 40%) and of 21 species duplicate accessions were included to check for correspondence between sequences. Eleven unidentified specimens were included because of some noticeable characters (e.g. the undescribed *Guatteria* sp. #5 is a liana from Peru, and only the second liana species besides *G. scandens*) and 7 'aff.' or 'cf.' specimens were used because no more accurately identified specimens were available. Samples were taken throughout the distributional range of the genus, representing both subgenera and 20 out of 22 sections as described by Fries (1959). Monotypic sections *Dimorphopetalum* (*G. dimorphopetala*) and *Cordylocarpus* (*G. clavigera*) were not sampled due to unavailability of material. As many as 23 type specimens, several belonging to species complexes, were sequenced in order to determine the closest affinity of several unidentified specimens falling within such complexes.

Of the satellite genera *Guatteriopsis, Guatteriella* and *Heteropetalum* (figure 1) mainly herbarium material was available (exceptions being one collection of *Guatteriopsis hispida* and one of *G. ramiflora*). For *Guatteriopsis* all five species could be included in this study (*Guatteriopsis blepharophylla*, *G. friesiana, G. hispida, G. kuhlmannii,* and *G. ramiflora*). For *Guatteriella* only *G. tomentosa* could be included and for *Heteropetalum* only *H. spruceanum*, due to problems with sequencing the remaining species from these two genera.

Genomic DNA extraction, PCR amplification and sequencing.

Total genomic DNA from fresh silica-dried leaves and herbarium specimens was extracted using a modified CTAB method (Doyle & Doyle, 1987). The *matK* gene was amplified and sequenced using primers 390F and 1326R (Cuénoud & al., 2002), 390F-2 (Erkens & al., chapter 4) and the internal MintF and MintR (Pirie & al., 2005b). For *rbcL* the primers 1F/724R (Olmstead & al., 1992), 636F/1460R (Fay & al., 1997; Fay & al., 1998) and 217F, 922F, 536R and 1104R (Pirie & al., 2005b) were used. The *trnT-trnF* region was amplified and sequenced using primers c, d, e and f (Taberlet & al., 1991). Finally, the *psbA-trnH* intergenic spacer was amplified and sequenced with primers psbA and trnH (Hamilton, 1999).

Figure 1. Representatives of the *Guatteria* group. A. Flowering branch of *Guatteria sp.* (*Maas & al. 8270*, U); B. Flowering branch of *Guatteriopsis blepharophylla* (*Harley & al. 10962*); inset shows close up of flower at anthesis and flower bud (*Maas & al. 8365*, U); C. Flowering branch of *Guatteriella tomentosa* (*Cid & al. 9987*, U; fruits of *Cid & al. 8547*, US); D. Flowering branch of *Heteropetalum spruceanum*. Photo credit: A and B, Paul Maas; D, D.W. Stevenson.

Generally, a standard PCR protocol (35 cycles; 30 sec.: 94°C, 30 sec.: 53°C, 1 min.: 72°C, with an initial 5 min.: 94°C and final 10 min.: 72°C) was used and 0.4% BSA was added to the mixes. PCR products were purified using the QIAquick PCR purification kit (Qiagen) and cycle-sequenced with DYE-ET (Amersham) or BIG-DYE terminators (Applied Biosystems) and run on an ABI 3730XL automated DNA sequencer.

Phylogenetic analyses

Outgroups were chosen on the basis of analyses by Richardson & al. (2004). Erkens & al. (chapter 4) compiled a matrix containing 43 *Guatteria* accessions (representing all putative larger clades in the genus) and sequence data from five plastid markers (*matK*, *rbcL*, *trnT-trnL*, *trnL-trnF* and *psbA-trnH*). The strict consensus tree resulting from phylogenetic analysis of this matrix was used as a backbone constraint on the larger matrix in this study, with 145 *Guatteria* accessions but only four plastid regions.

Most-parsimonious trees were generated from 10,000 replicates of random taxon addition and swapped using tree bisection-reconnection (TBR), equal weights and a maximum of 10 trees held at each step, using PAUP* 4.0b10 (Swofford, 2003). A bootstrap analysis (Felsenstein, 1985) of 10,000 replicates with "full" heuristic searches was performed using 10 random addition sequences with equal weights, TBR swapping, saving a maximum of 5 trees at each replicate. Bootstrap support of 50-74% is considered to represent weak support, 75-89% moderate support and 90-100% strong support.

The data were also analysed with Bayesian inference using MrBayes version 3.1.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) analyses were run for 2,500,000 generations with four simultaneous Monte Carlo Markov Chains, and one tree sampled per 100 generations. Parameters for the general DNA substitution model (GTR with gamma-distributed rate variation across sites) for the separate partitions were estimated by MrBayes. All partitions were allowed to have their unique model and the overall evolutionary rate was allowed to be (potentially) different across partitions. Only parsimony informative characters were coded as indels and MrBayes was informed of this coding bias in order to calculate the probability of the data correctly (using the "lset coding=informative" option).

Wood anatomical data

Much information on the *Guatteria* group is available, such as data on flower anatomy (van Heusden, 1992), fruit and seed morphology (van Setten & Koek-Noorman, 1992), karyology and cuticular folding patterns (Morawetz & Waha, 1985), pollen (Walker, 1971; Morawetz & Waha, 1985), and oil composition (Maia & al., 2005). Data on the wood anatomy of the *Guatteria* group are sparse. Although wood anatomy of Annonaceae is highly homogeneous, *Guatteria* stands out as a genus that can be recognised on the basis of a combination of characters (Westra & Koek-Noorman, 2003). In the light of the homogeneity in the family, possible wood anatomical differences between the genera of the *Guatteria* group can be regarded as important additional data. For the wood anatomical part of this study 17 species of *Guatteria* were studied (representing different clades in the tree in figure 2, see also table 1) and one species of *Guatteriopsis*, *Guatteriella* and *Heteropetalum* each (table 1). All wood samples were obtained from the Wood Collection of the Nationaal Herbarium

Table 1. Selected wood anatomical features of representatives of *Guatteria*, *Guatteriella*, *Guatteriopsis* and *Heteropetalum*. Uw-number: Utrecht Wood identification number. Clade names are those shown in figure 2 (if no clade name is given, the species was not included in the phylogenetic study).

				VESSELS			PARENCHYMA		RAYS		
Species	**Uw-number**	**Country**	**Collector**	diameter in µm	arrangement	number per sq. mm	apotracheal bands (nr. per mm)	paratracheal; width of rings (nr. of cells)	number per mm (transv. sect.; nr. per mm)	width (nr. of cells)	**Clade**
G. alta R.E.Fr.	Uw 25132	Colombia	Cuatrecasas 14829 (paratype)	175-220	> 50% solitary	3-8	11-12	1-2	1-3	6-8	CAC
G. anomala R.E.Fr.	Uw 36880	Mexico	Ishiki, M. 2233	60-80	many clusters	19-24	13-15	absent	2-3	10-13	subgenus *Anomalantha*
G. blainii (Griseb.) Urb.	Uw 31215	Dominican Republic	Maas 6443	90-120	predomin. solitary	2-8	10-12	1-2	2-3	5-6	section *Dolichocarpus* s.s.
G. conspicua R.E.Fr.	Uw 1241	Suriname	Lanjouw & Lindeman 455	120-160	< 50% solitary	5-7	8	1-2	2-3	4-6	--
G. curvipetala R.E.Fr.	Uw 7806	Brazil	Krukoff 6600	240-300	predomin. solitary	2(-3)	ca 10	1-3	2-3	6-7	--
G. discolor R.E.Fr.	Uw 8134	Brazil	Krukoff 7047 (type specimen)	-300	> 50% solitary	1-2	7-8	1-2	4	6-8	SAC
G. dusenii R.E.Fr.	Uw 13675	Brazil	Lindeman & Horreus de Haas 2330	80-160	predomin. solitary	2-3	?	1(-2)	3-4	-10	SAC
G. elegantissima R.E.Fr.	Uw 25071	Colombia	Cuatrecasas 17028 (paratype)	175-250	> 50% solitary	3-6	8-10	1(-2)	2-3	6-8	CAC
G. monticola R.E.Fr.	Uw 34268	Guyana	FDBG5882 (Wilson-Browne 473; type specimen)	100-200	predomin. solitary	6-7	?	1	6-7	-5	--
G. obovata R.E. Fr.	Uw 29461	Brazil	Morawetz 16-18883	100-150	50% solitary	3-5 (2-7)	9-12	1-2	3-4	3-5	--
G. poeppigiana Mart.	Uw 17242	Brazil	Maguire 51863	160-200	50% solitary	3	ca 8	1-2	2-3	-7	SAC
G. procera R.E.Fr.	Uw 2567	Suriname	Maguire 24684	120-200	predomin. solitary	4	7-8	1-2	5	7-9	--
G. punctata (Aubl.) R.A. Howard	Uw 34267	French Guyana	Prévost & Bartélémy 3688	160-200	predomin. solitary	1	5?	1-2 c wide	2?	8	SAC
G. punctata (Aubl.) R.A. Howard	Uw 2565, 2566	Suriname	Maguire 24430, 24589	80-200	50% solitary	5-7	11	1-2	2-3	6-8?	SAC
G. rubrinervis R.E.Fr.	Uw 34270	Guyana	FDBG 5816 (Wilson Browne 417; type specimen)	160-240	predomin. solitary	3-4	10	1-3	3	5-6	--
G. scandens Ducke	Uw 24786	Guyana	Maas & Westra 3600	100-250	50-90% solitary	6-10	9-15	p.p.(vasic).	2-4	-10	LBC
G. schomburgkiana Mart.	Uw 254, 267, 2568, 8841	Suriname	Stahel 254, 267; Schulz 8925	200-300	< 50 % solitary	3-4 (-8)	7-8	1(-3)	3-4	5-7	SAC
G. trichostemon R.E.Fr.	Uw 16119	Brazil	Krukoff 8862	200-280	predomin. solitary	2	9-10	1-2	3(-4)	6-7	--
Guatteriella campinensis Morawetz & Maas	Uw 29468	Brazil	Morawetz 31-24883	160-200	exclusiv. solitary	1-3	7-8	1-2	(1-) 2	5-8	*Guatteriella*
Guatteriopsis hispida	Uw 29458	Brazil	Morawetz 12-25883	100-150	50% solitary	3-5 (2-7)	9-12	1-2	3-4	3-5	*Guatteriopsis* # 1
Heteropetalum brasiliense Benth.	Uw 33073	Brazil	Stevenson 1115	80-100	predomin. solitary	2 (0-4)	7-9	few strands	2-4	3-5	*Heteropetalum*

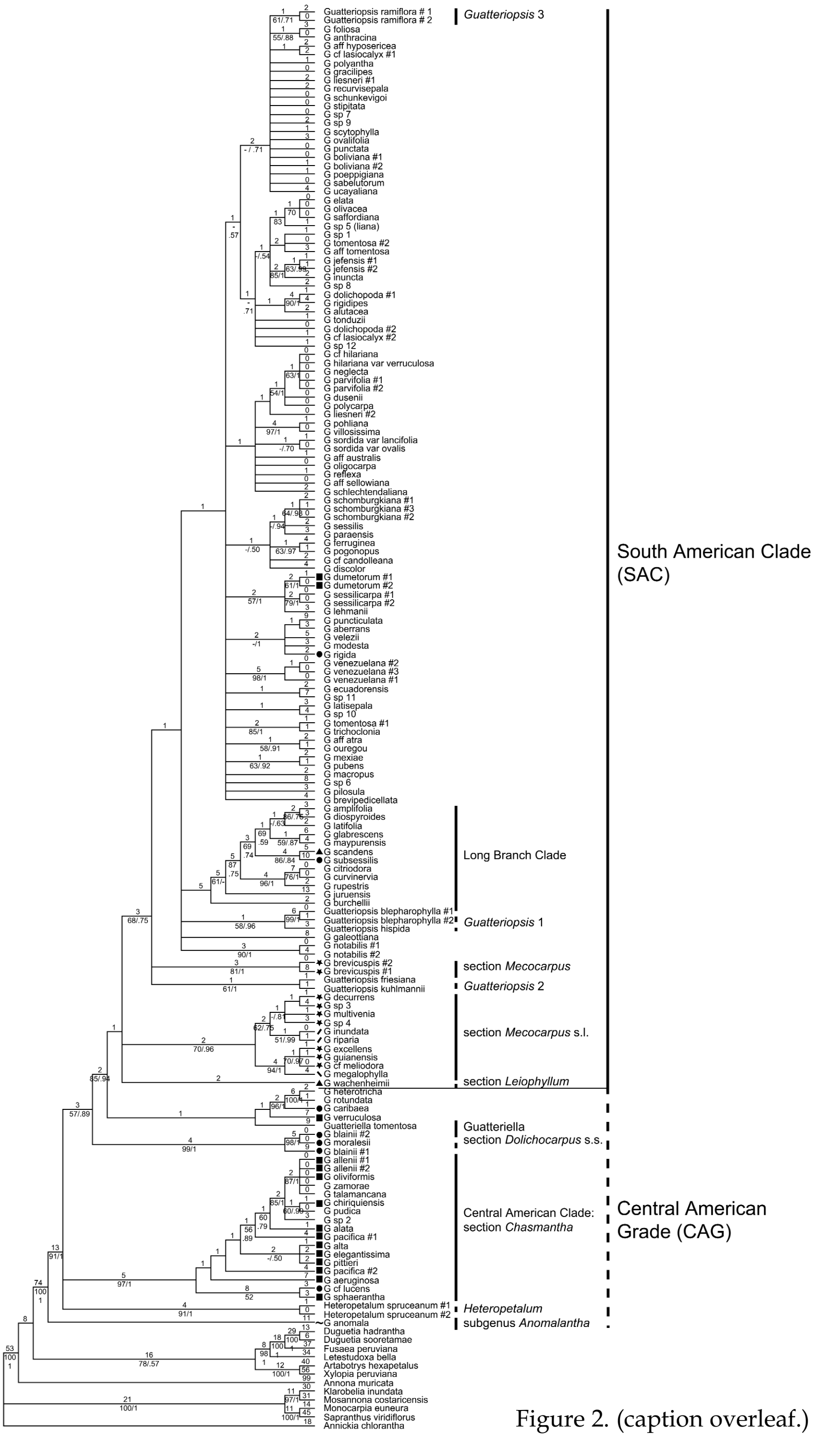

Figure 2. (caption overleaf.)

Nederland, Utrecht University Branch (U). All samples are backed by herbarium vouchers, identified by several *Guatteria* specialists. The wood sections were prepared according to standard techniques and stained with saffranin. Terminology is according to the List of Microscopic Features for Hardwood Identification (IAWA Committee, 1989).

RESULTS

For all accessions the *matK*, *rbcL*, *trnL-trnF* and *psbA-trnH* plastid DNA regions were sequenced, with the exception of some accessions for which no or only partial sequences of certain regions were obtained (appendix 1).

Phylogenetic relationships

Phylogenetic analysis resulted in 41,610 most parsimonious trees of 1180 steps, with a consistency index (CI) of 0.71 and retention index (RI) of 0.86. One of the most parsimonious trees is shown in figure 2. Sequence variation is almost limited to basal branches in *Guatteria* with very little or no variation among members of the large South American Clade. This results in generally weakly or unsupported clades, except for the basal part of the cladogram.

Guatteria, including its smaller satellite genera, is a well supported monophyletic group with bootstrap support (BS) of 100% and a posterior probability (PP) of 1.0 and is subtended by a long branch of 74 substitutions. The most basal lineage and sister to the rest of the genus is *Guatteria anomala*. The genus *Heteropetalum* (BS 91%; PP 1.0), species of *Guatteria* section *Chasmantha sensu* Fries (1959; BS 97%; PP 1.0), and the remaining species (BS 57%; PP 0.89) appear as a polytomy. *Guatteria blainii*, a species from the Caribbean Islands and part of section *Dolichocarpus* does not appear as monophyletic; one of the accessions forms a separate lineage (BS 99%; PP 1.0) with *Guatteria moralesii* (BS 98%; PP 1.0). Next to several species pairs or trinities of species, only few other terminal clades receive BS > 50%. Most of the species of *Guatteria* section *Mecocarpus* form a weakly bootstrap supported clade but this relationship is strongly supported by the Bayesian analysis (BS 70%; PP 0.96). The monotypic section *Megalophyllum* and representatives of section *Stenocarpus* are nested within section *Mecocarpus*. A clade that shows much sequence variation and thus long internal branches is the so called Long Branch Clade (LBC). It consists of morphological very different species and contains accessions from ten different sections. The inclusion of *Guatteria burchellii* is not supported and the inclusion of *G. juruensis* only with 61% BS (and unsupported by PP). Their position is therefore doubtful. The remainder of the species form a moderately supported monophyletic group (BS 87%, PP 0.75).

The species of *Guatteriopsis* do not prove to be monophyletic, but monophyly is not definitively refuted either given lack of support values of the nodes separating the three clades. The genus separates into three lineages: (1) *Guatteriopsis blepharophylla* with *G. hispida* (BS 58%, PP 0.96); (2) *G. friesiana* with *G. kuhlmanii* (BS 62%, PP 1.0); and (3) two accessions of *G. ramiflora* (BS 61%, PP 0.71).

Figure 2 (previous page). One of 41,610 most parsimonious trees from an analysis based on plastid *matK*, *trnLF*, *rbcL* and *psbA-trnH* sequences. Branch lengths are shown above the branches, bootstrap percentages and Bayesian posterior probabilities below. Sections discussed in text are indicated before the species names, symbols indicate section *Chasmantha* (■), *Dolichocarpus* (●), *Leiophyllum* (▲), *Mecocarpus* (✶), *Megalophyllum* (\) or *Stenocarpus* (/), and subgenus *Anomalantha* (~). Clade names are those referred to in the text.

Guatteriella is sister to a clade containing four species of *Guatteria* but this relationship is not supported.

Wood anatomy of Guatteria s.l.

In most *Guatteria* species studied here, vessels are large, up to 150-300 µm (table 1). Often, a predominance of solitary vessels is found. There are few multiseriate rays, up to 10 cells wide, often no more than 1-3 per mm; uniseriate rays are scanty or absent. Parenchyma bands, 1-3 cells wide and up to 12 per mm, are often conspicuous as the adjacent fibres have a relatively wide lumen. Besides, careful observation of very smooth end grain surfaces will reveal narrow rings of vasicentric parenchyma around the vessels.

In one of the climbing species in this study, *Guatteria scandens*, a more or less gradual transition from narrower to wide vessels is found when going away from the centre. This ultimately leads to tangential parenchyma bands becoming indistinct, although they remain present. As a result, the characteristic "annonaceous" wood pattern is therefore obvious only in the central part of the stem of this climber, but becomes slightly disrupted toward the periphery.

In *Heteropetalum* paratracheal parenchyma is restricted to a few strands: showing in cross section as an incomplete vasicentric sheath, or rarely a vasicentric sheath of one cell wide at most. Fibres are extremely thin-walled. Rays are up to 5 cells wide. Vessels are few: 0-10 per mm^2, and at the same time extremely narrow (80-100 mu). This combination of few, narrow vessels and thin-walled fibres may be due to the very wet habitat conditions of the *Heteropetalum* species.

DISCUSSION

Monophyly

To test for monophyly of a genus a high taxon sampling is important (Barraclough & Nee, 2001). So far, alliance between the genera in the *Guatteria*-group has been tested using only one representative per genus. Bygrave (2000) recovered a sistergroup relationship between two accessions of *Guatteria* and *Guatteriopsis* respectively, which were the only genera sampled in his phylogenetic study based on *rbcL* sequence data. He (1999) retrieved a monophyletic group comprising all four genera, in an analysis of morphological characters scored at the genus level. Although showing their alliance, the latter two studies did not contribute to our understanding of the relationships between *Guatteria* and its satellite genera.

Here c. 40% of the described *Guatteria* species have been sampled and all species of *Guatteriopsis* are included. Unfortunately, still only one out of two species of both *Heteropetalum* and *Guatteriella* could be incorporated. Nonetheless, because of the greater sampling within *Guatteria* it is possible to investigate the relationships of the genera in the *Guatteria* group in greater depth.

Guatteria is a well supported monophyletic genus (figure 2), as was found in previous phylogenetic studies with lower taxon sampling as well (Richardson & al., 2004; Pirie & al., 2005b; Erkens & al., chapter 4). Furthermore, *Guatteriopsis*, *Guatteriella*, and *Heteropetalum* are all nested within *Guatteria*, the four genera together comprising a monophyletic assemblage subtended by a long branch of 74 substitutions. This long branch raises the issue of possible incomplete taxon sampling. Based on Richardson & al. (2004) and further taxon sampling (Chatrou & al., unpublished data), however, no taxa were found that could break up this branch. This unambiguously confirms the earlier hypothesised, morphology based, close relationship between these genera.

Guatteriopsis

All species of *Guatteriopsis* are well nested within *Guatteria* (figure 2) and generic status is therefore unjustified (as was already suggested by Morawetz & Waha, 1985; van Heusden, 1992). This conclusion is further supported by recent oil composition analysis (Maia & al., 2005) and wood anatomical characters (see below). Monophyly of the species was expected on the basis of morphological characters but this expectation could not be confirmed, nor refuted here. *Guatteriopsis* is divided into three separate lineages: (1) *Guatteriopsis blepharophylla* with *G. hispida*; (2) *G. friesiana* with *G. kuhlmanii;* and (3) *G. ramiflora*. Although BS and PP values for the presented topology are low, no single analysis (or data partition) yielded a monophyletic *Guatteriopsis*-clade.

Guatteriopsis blepharophylla and *G. hispida* were described first and they represent the 'archetype' of the genus. They possess flowers on short pedicels, valvate petals and an articulation nearer to the flower when compared to *Guatteria*. *Guatteriopsis friesiana* and *G. kuhlmanii* were added later to the genus and both species have a rounded to cordate leaf base which separates them from *G. blepharophylla* and *G. hispida*. Furthermore, the flower morphology of *G. friesiana* is aberrant from that in other species of *Guatteriopsis* (this is not the case for *G. kuhlmanii*). Lastly, *Guatteriopsis ramiflora* "[…] differs markedly from the other species in the genus […]" as stated in the original description (Simpson, 1982). Indeed, on the basis of the three above mentioned flower characteristics this species has erroneously been described in *Guatteriopsis*: the petals are imbricate, the pedicel is 2.5-4 cm long (in *Guatteriopsis* <1 cm) and the articulation is suprabasal. Therefore, this species should not have been described as *Guatteriopsis* and monophyly with the other species of *Guatteriopsis* is not expected. If still proven monophyletic for the other four species, *Guatteriopsis* would at best represent a section of *Guatteria*.

More data is needed for definitive conclusions about the phylogenetic position of the different *Guatteriopsis* species and their closest relatives. For instance, *Guatteriopsis* is said to be distinct by its valvate petals but in *Guatteria* section *Megalophyllum* intermediate specimens were found between *Guatteria* and *Guatteriopsis* (van Heusden, 1992). On the basis of the results obtained here a close relationship to certain species of this section cannot be ruled out yet (see below).

Guatteriella

Only one out of two species of the rare and little known genus *Guatteriella* could be included in this study due to the lack of freshly collected material. Therefore it is impossible to investigate the monophyly of this genus. On the basis of morphology (i.e. the laterally flattened, hairy monocarps, thick and densely hairy, brownish yellow petals, and the percurrent straight tertiary leaf venation) monophyly is expected, though. As *Guatteriella tomentosa* is nested within *Guatteria*, *Guatteriella* should not be maintained as a separate genus. More sequence data, and the sampling of *G. campinensis*, is needed to determine its closest relatives and to establish if *Guatteriella* should be treated as a separate section within *Guatteria*.

On the basis of the slightly imbricate inner petals (outer ones valvate) of *Guatteriella*, it has been suggested that the genus holds an 'intermediate position' between *Guatteriopsis* (valvate petals) and *Guatteria* (imbricate petals; Fries, 1939; Morawetz & Maas, 1984). Apart from the ambiguous meaning of 'intermediate' in a phylogenetic context, it can be concluded that the current (unsupported) placement of *Guatteriella* rules out such a hypothesis with respect to floral character evolution (figure 2).

Heteropetalum

Heteropetalum is the only Neotropical Annonaceae genus with outer petals as small as the sepals (van Heusden, 1992). Only one out of two species was included in this study but this might not pose a problem with regard to monophyly. *H. brasiliense* en *H. spruceanum* are very closely related (Fries, 1959b) and it may be more correct to unite them into one species (as was for instance preliminary done by Steyermark & Berry, 1995). Because of the similar morphology of the two *Heteropetalum* species and their aberrant flower morphology in comparison to *Guatteria* it is reasonable to expect that *H. brasiliense* indeed forms a clade with *H. spruceanum*. *Guatteria dimorphopetala* also shows greatly reduced outer petals and therefore is placed in the monotypic section *Dimorphopetalum*. The relationship between *G. dimorphopetala* and *Heteropetalum* is unknown because the former is not included in this study. However, no close relationship is expected because the flower morphology of *G. dimorphopetala* is different and it does not have the typical *Heteropetalum* ecology (occurrence in inundated regions), which is otherwise rare in *Guatteria*.

Looking at the phylogenetic position of *Heteropetalum* (taking into account the subgenus *Anomalantha*; see below) and its clearly aberrant morphology in comparison to *Guatteria* it is proposed here to erect a third clearly distinguishable subgenus, *Heteropetalum*.

The phylogenetic position of *Heteropetalum* is surprising. It is nested in the so-called Central American Grade (CAG; Erkens & al., chapter 4), a grade that so far accommodated only species from Central America, the Caribbean and some species from west of the Andes in Colombia. Because the ancestors of *Heteropetalum* were presumably located in Central America (based on optimisation of geographical areas, data not shown), its placement might indicate a mid- to late-Miocene dispersal into South America, based on age estimates in Erkens & al. (chapter 4).

The morphology of *Heteropetalum* is different when compared to the general *Guatteria* 'archetype', but falls within the variation of the genus. *Heteropetalum* might have diverged from the general *Guatteria* 'archetype' after migration into South America or this 'archetype' only developed after the split from *G. anomala* and *Heteropetalum*. On the basis of the aberrant morphology of *G. anomala* (see below) and *Heteropetalum*, the latter is expected. In its wood anatomy, *Heteropetalum* differs from *Guatteria* and the great majority of Annonaceae, a.o. because of the lack of vasicentric parenchyma. If more data would indeed show *Heteropetalum* to have diverged before the Central American Clade, one could hypothesise that *G. anomala* might also possess different wood anatomical characters in comparison to the other *Guatteria* species. This would be anatomical evidence to support the thesis that the *Guatteria* 'archetype' indeed evolved after the divergence of *G. anomala* and *Heteropetalum*.

Wood anatomy of Guatteria s.l.

The wood of the genus *Guatteria* conforms to the general pattern of Annonaceae (Metcalfe

& Chalk, 1987; Koek-Noorman & Westra, unpublished data). The highly homogeneous family of Annonaceae is easily recognised by the cobweb-like pattern in transverse section, formed by rays and parenchyma. The often wide rays consist of procumbent cells with 1-4 rows of marginal cells, the apotracheal parenchyma is arranged in regular, narrow, 1(-3) cells wide bands. When using these characters, consultation of the website Inside Wood (Wheeler & al., 2004-onwards) results in a list of mainly Annonaceae together with only few other genera. Adding a few more characters which can easily be seen with a hand lens, like number and diameter of the vessels, will reduce the number of alternatives even further (Westra & Koek-Noorman, 2003).

The high homogeneity of wood-anatomical features makes it difficult or even impossible to recognise most genera of the family. However, *Guatteria*, though not showing unique character states, seems to stand out as one of the few large genera that can be recognised on the base of a combination of characters. The narrow, complete rings of vasicentric parenchymna around the vessels in particular, found in all species of *Guatteria* but *G. anomala* (table 1), are rather uncommon in Annonaceae. If present, paratracheal parenchyma is mostly restricted to few strands or incomplete rings. This was found in some genera of the basal Canangoids (e.g. *Cananga, Cyathocalyx, Tetrameranthus*) and few species of other genera, among which *Mezzettia* (Metcalfe & Chalk, 1987Koek-Noorman & Westra, in prep.). The small satellite genera *Guatteriella* and *Guatteriopsis* show vasicentric rings as well. In all other characters, their wood anatomical structure falls within the variation shown by *Guatteria*. Their phylogenetic position, nested within *Guatteria*, therefore is also supported by their wood anatomy.

In contrast to that of *Guatteria*, paratracheal parenchyma in *Heteropetalum* is found as incomplete rings, or few strands. In figure 2 *Heteropetalum* is found near *Guatteria anomala* at the base of a grade accommodating the majority of *Guatteria* species, *Guatteriopsis* and *Guatteriella*. In *Guatteria anomala*, vessels are no more than 60-80 µm wide, c. 20 per mm^2, mostly arranged in multiples or clusters of 2-5(-8) cells. Paratracheal parenchyma is absent, or restricted to few strands only. Complete vasicentric sheaths were not observed.
These character states, although not typical for the *Guatteria* clade, are very common for the family as a whole. Thus, the occurrence of these character states in *Guatteria anomala* as well as *Heteropetalum* seems to suggest an intermediate position of both between *Guatteria* and the other Annonaceae. This supports their basal position in figure 2. It also suggests a more basal position of *Heteropetalum* with respect to section *Chasmantha* (of which the species posses vasicentric parenchyma; table 2), a relationship not supported by molecular data so far. With regard to morphological evolution, it therefore seems that the characters used to delimit the genus *Guatteria* (its archetype) evolved after the split of *Guatteria anomala* and *Heteropetalum.*

Fries' section circumscription

The use of infrageneric sections can be criticised especially when they are solely based on morphological similarities that might show high levels of homoplasy. In the last and only revision of *Guatteria* (1939) Fries stated that: "Some of the 30 mentioned sections are definitely not entirely natural" and his attempt to circumscribe sections should only be seen as provisionally. Twenty years later he himself reduced the number of sections to 22, merging several ill described ones (Fries, 1959b). However, he still stated that the systematic arrangement of the species remained problematic because of the fact that of many species fruits and flowers were unknown to him. Fries' revision and additions are the most comprehensive work on the genus so far and his sections are used as a general reference, as if they only constitute closely related species. However, his classification is phenetic and not one based on the (at that time unknown) concept of monophyletic groups. Therefore, the monophyly of the sections is investigated here to find out if his sections indeed can be used as a guideline and general reference or that they constitute non-monophyletic groupings. The cladogram obtained in this study does not allow for definite conclusions on all sections since many relationships are poorly or un-supported. Nevertheless, as a starting point for evaluation it is possible to investigate clades more basal in the tree since these are well supported.

Especially in a large and morphologically complex genus as *Guatteria* sections are of particular importance. Not because they have any special biological meaning but because they enhance the systematic research on the group. The recognition of well supported subgeneric monophyletic groups maximises stability of classification, phylogenetic information, and ease of identification (Backlund & Bremer, 1998). For instance, if a specimen cannot be identified to name (e.g. *G. sp.* A) it can be very useful to at least categorise it into a certain (monophyletic) section (e.g. *G. sp.* A section *Chasmantha*). The large genus can so be subdivided in smaller more comprehensible clades and because of their monophyly each of these can serve as focal points for further phylogenetic and morphological study.

Guatteria anomala: the monotypic subgenus Anomalantha

n his 1955 addition to his 1939 revision, Fries recognised two subgenera: *Anomalantha* and *Guatteria*. Section *Anomalantha* is monotypic and only holds *Guatteria anomala* (section *Guatteria* contains all other species in the genus). *Guatteria anomala* is found here to be the earliest branching lineage within *Guatteria* and sister to the rest of the genus (figure 2). The morphology of the monocarps of *G. anomala* resembles that of the species in section *Chasmantha* well (see below; Fries, 1939). However, based on its isolated phylogenetic position and anomalous morphological characters such as the terminal, branching inflorescence, wood anatomical characters (see above), and its much larger growth form (trees up to 60 m), it is phylogenetically and systematically well separated from the other species of *Guatteria* and rightly placed in a subgenus.

The Central American Clade: section Chasmantha

The etymology of the section name "*Chasmantha*" is unclear (Fries, 1939; 1950a; 1959). It could be derived from the fact that the petals usually stay horizontal until anthesis (after which they close; so called open-flower bud development) but this character is not specific for the species in this section. Another explanation could be that the flower buds open via a crevice but this character does not at all occur in *Guatteria*. This lack of nomenclatural clarity mirrors the uncertainty about the morphological synapomorphies uniting the species of section *Chasmantha* (Fries, 1939; 1950a; 1959). All the species in this section occur in Central America (Guatemala - Panama) and the adjacent part of Colombia (west of the Andes) and were probably ascribed to this section on the basis of their occurrence rather than on the basis of one or another morphological character. Also in a later revision of this section (Sánchez S., 1986) no synapomorphies for the section as a whole are mentioned.

Notwithstanding these obscurities, it is clear that this section is almost completely monophyletic (figure 2) with the exception of *Guatteria dumetorum* and the type specimen of *G. verruculosa*. These species were apparently erroneously placed in section *Chasmantha* (Fries, 1950a; 1955b). Both are included based on the fact that their leaves are densely verrucose on both sides (one-sided verrucose leaves being a character delimiting a subsection within section *Chasmantha*). *G. verruculosa* is known from the Cordillera Central in Colombia and thus occurs at the border of the distribution of the other Colombian species in section *Chasmantha*. The current phylogenetic placement of this species is unsupported but it is clearly unrelated to the other species in section *Chasmantha*. Morphologically it probably can be connected to the species it is placed sister to (see below).

Guatteria cf. *lucens* is an accession from Panama and according to this analysis should be placed in section *Chasmantha* with the other Central American species. This specimen was for a long time the only putative representative of this poorly known and rarely collected species. According to Fries (1959) *G. lucens* should be placed in section *Dolichocarpus* (Fries, 1950a). However, ongoing taxonomic work on all Central American *Guatteria* species is indicating overlap between (newly discovered specimens of) *G. lucens* and *G. dumetorum* and it is likely that both species will be united. The specimen *G.* cf. *lucens* that is used in this study is somewhat aberrant from the recognised *G. lucens*. Although falling within the variation of *G. lucens*, it has for instance a raised primary vein on the upper side of the leaf, while the type of *G. lucens* has an impressed primary vein. Unfortunately no other material of this species was available for molecular work. The deviant morphology and its phylogenetic placement in section *Chasmantha* might therefore indicate that this specimen is not representative for *G. lucens* after all.

Guatteria blainii: section Dolichocarpus

All species from section *Dolichocarpus* are sampled in this study and figure 2 shows that this section is not a natural one. Fries (1959) distinguishes three groups, one consisting of *Guatteria blainii* with *G. moralesii*; the second of *G. caribaea* with *G. rigida* and *G. lucens;* and the last solely comprising *G. subsessilis*.

Guatteria blainii and *G. moralesii* form a separate clade (figure 2), but the two accessions of the former species do not prove to be monophyletic. *G. blainii* #2 from Cuba is sister to the type specimen of *G. moralesii* (also from Cuba). Both accessions have larger leaves and are generally trees. This clade is relatively divergent from the second accession of *G. blainii* from the Dominican Republic, which is small-leaved and a treelet. Cuban specimens of *G. blainii* should therefore be re-examined to investigate if these should be incorporated into *G. moralesii*.

Guatteria caribaea, *G. rigida*, *G. lucens*, and *G. subsessilis* are not related at all (figure 2) and it is clear that the classification of these species into a single section is untenable. In this group of species, *G. caribaea* is the only one occurring on the Caribbean islands but it is not closely related to *G. blainii*. Next to clear morphological differences between these species, *G. caribaea* shares molecular synapomorphies with the South American species of *Guatteria*, while *G. blainii* shares molecular characters with the Central American ones. *G. caribaea* is strongly supported as sister to *G. heterotricha* from Colombia (section *Sclerophyllum*) and *G. rotundata* (unplaced) from Panama. The latter two species only differ in a few morphological characters and further morphological study might reveal synapomorphies for these species with *G. caribaea*. Furthermore, the unsupported phylogenetic position of *G. verruculosa* as sister to these three species (see above) might morphologically be supported by characters such as leaf shape and shortly stipitate monocarps. However, because only the type of *G. verruculosa* could be studied no conclusions can be drawn yet. The phylogenetic position of *G. rigida* remains unclear but *G. subsessilis* is well nested within a moderately supported clade (see below).

Guatteria wachenheimii: section Leiophyllum

Section *Leiophyllum*, comprising only *Guatteria scandens*, *G. conspicua* and *G. wachenheimii* (Fries, 1959b), can safely be regarded as non-monophyletic. The sampled species (*G. scandens* and *G. wachenheimii*) are not closely related. *G. scandens* is well nested within a moderately supported clade (see below), while *G. wachenheimii* is positioned at the base of the SAC (figure 2). The species were united in this section on the basis of having thick leaves and a marginal vein but no monocarps were seen. Therefore, at the time the affiliation of the species could not unambiguously be assured. Now it is known that *G. wachenheimii* has shorter stipes and smaller monocarps than *G. scandens* and that the latter does not have a clear marginal vein.

G. conspicua (a tree) agrees in leaf type and flowers (especially the connective shield) with the liana-species *G. scandens* (Fries, 1950b). Furthermore, it has flowers on the leafy twigs as well as on the trunk, as *G. scandens*. It shares shortly stipitate, smaller monocarps with *G. wachenheimii* but this character should be attributed little weight because several unrelated species have similar sized monocarps. Based on gross morphology therefore *G. conspicua* is expected to be more closely related to *G. scandens* than to the more morphologically divergent *G. wachenheimii*.

Amazonian clade: section Mecocarpus s.l.

Section *Mecocarpus* is characterised by (large to very large) warty leaves in combination with oblong and short stiped monocarps and a marginal vein. It is paraphyletic with respect to sections *Megalophyllum* and *Stenocarpus*. The monospecific section *Megalophyllum* can only be distinguished from section *Mecocarpus* because the leaves of *Guatteria megalophylla* lack warts, monocarp shape and stipe length are roughly the same. Section *Megalophyllum* could therefore best be united with the latter section into section *Mecocarpus* s.l.

Some specimens from section *Megalophyllum* have been reported to be morphologically intermediate between this section and *Guatteriopsis* on the basis of flower characters (van Heusden, 1992). However, no phylogenetic relationship seems to exist (figure 2) and the investigated characters might therefore show homoplasy.

The species of section *Mecocarpus* s.l. form a monophyletic group with two species of section *Stenocarpus* (*Guatteria inundata* and *G. riparia*). Characteristic for the species of section *Stenocarpus* are the shortly stipitate, large fusiform monocarps, leaves with a clear marginal vein and their growth in inundated regions. At first sight there is no clear morphological character to group section *Stenocarpus* with section *Mecocarpus* s.l. However, in Fries' 1939 key, sections *Megalophyllum* and *Stenocarpus* are united on the basis of having leaves with a clear marginal vein, shortly stipitate monocarps, and papillate connective shields. It is clear from figure 2, however, that these characters are homoplasious because these sections are not sister to each other. Several clear differences exist, sections *Mecocarpus* s.l. and *Stenocarpus* can be separated on the basis of large coriaceous leaves versus smaller thin leaves and long versus shortly pedicilate flowers (for section *Mecocarpus* s.l. and *Stenocarpus* respectively). The other species of section *Stenocarpus* (*G. dolichophylla*, *G. obovata, G. oblanceolata,* and *G. phanerocampta*) were not sampled but should probably be united with *G. riparia* or *G. inundata* because of their highly similar morphology. On the basis of the results obtained here it can therefore be concluded that sections *Mecocarpus* s.l. and *Stenocarpus* should be merged into a new section.

It is obvious that the morphological circumscription of sections *Mecocarpus* s.l. and *Stenocarpus* together needs more attention. Conversely, it is possible to unite these sections on the basis of their distribution. Both sections are mainly found in the Amazon basin. Unfortunately, more sections have their main diversity in that area since roughly half of all *Guatteria* species occur there.

Species of section *Mecocarpus* as described by Fries (1939) are easily recognisable and monophyly of all its species was expected. Surprisingly this is not the case. Our data indicate that two accessions of *Guatteria brevicuspis* form a separate clade. Though still poorly supported, they are more closely related to *Guatteriopsis* than to the remainder of section *Mecocarpus*. It is unclear on the basis of what characters these two accessions can morphologically be separated from the rest of the species of section *Mecocarpus*. However, it is obvious that these specimens resemble *Guatteriopsis blepharophylla* on the basis of leaf and monocarp morphology (no flowers were seen). Only six out of 20 species of section *Mecocarpus* were included in this study and therefore no definitive conclusions can be drawn. Taxon sampling should be increased in order to gain more insight in the evolution of this almost monophyletic section.

Long Branch Clade

n comparison to other clades in the SAC the LBC has longer internal branches. The twelve species in this clade are assigned to ten different sections (*Guatteria rupestris* was never assigned to a section and *G. amplifolia* and *G. diospyroides* might be considered one species). The clade comprises some interesting species. *G. burchellii* is cauliflorous, a rare state in *Guatteria* and *G. scandens* is the only described liana-species in the genus (and also cauliflorous). *G. amplifolia* (including *G. diospyroides*) is the only non South American species in this clade and a recent invader of Central America (Erkens & al., chapter 4). The LBC should be further investigated to determine its sistergroup, to elucidate the cause for the apparent higher rate of molecular evolution and to search for morphological synapomorphies that link these morphologically very different species.

Evolution of the Guatteria group

Up to now no clear idea existed about the evolutionary relationships among the genera in the *Guatteria* group and between the species within *Guatteria*. Fries' revision and section circumscriptions were therefore always used as a framework. The data presented here show that *Guatteriopsis*, *Guatteriella* and *Heteropetalum* should be united with *Guatteria*.

Taxonomically speaking, *G. anomala* and *Heteropetalum* (after its submergence into *Guatteria*) could be put into their own subgenus because of their aberrant morphology and phylogenetic position. *Guatteriopsis* and *Guatteriella* should be submerged into *Guatteria* but a decision on a new status, for instance as a well circumscribed monophyletic section within *Guatteria*, is still premature due to a lack of phylogenetic support. Interestingly, most synapomorphies of *Guatteria* may have evolved only after the divergence of *G. anomala* and *Heteropetalum*.

With regard to Fries' sections, it can be concluded that most of them are probably non-monophyletic but the poorly resolved cladogram does not allow for definite conclusions on most of them since many clades are weakly or unsupported. Therefore, new section descriptions for a complete infrageneric classification of *Guatteria* would be premature.

Guatteria is the largest Annonaceae genus and one of the largest Neotropical tree genera. Because of its morphological homogeneity it proved very difficult to postulate key innovations that might have contributed to the speciation of the genus. There seems to be no relationship between the number of species (the species-richness) and the amount of adaptive diversity displayed. In addition, the lack of phylogenetic structure is problematic because it hampers the effective search for the sparse morphological and anatomical characters that could reflect the major groupings within the genus. Furthermore, even for well supported clades it still proves very difficult to pinpoint morphological synapomorphies and some clades seem to be more distinguished by geography than by morphology (Erkens & al., chapter 4). It has already been shown that large species-rich radiations may show extremely high levels of homoplasy on account of repeated re-assortment of the same character states in similar allopatric environments (Sanderson, 1998). This might also be the case in *Guatteria*, especially when taking into account that the genus' main mode of speciation might be ecological or by plain vicariance (Erkens & al., chapter 4). The morphological homogeneity might be the key to success for the genus. Because there is a lack of apparent specialisation, the genus might stay morphological versatile (Vermeij, 1973) and might be able to enter new adaptive zones more easily.

Several sorts of data are desirable for gaining further insight in the evolution of the genus. Data on seeds might be useful because the structure of the seed seems to be quite variable. Furthermore, articulation architecture and the ratio between the length of the pedical below and above the articulation might contain information. Also ecological data such as attracted pollinators, soil type and habitat information could be useful. Lastly, chemistry might be worthwhile to look at because there is a fair amount of variation in chemical composition (e.g. Maia & al., 2005). Although *Guatteria* is a common genus not much of this information is available.

This study can be used as a framework for future research. Putative clades have been identified and therefore it is now possible to target each of those clades at a time. Next to adding more sequence data, an important step is to increase taxon sampling by adding crucial but so far unsampled species (Barraclough & Nee, 2001), such as additional species from section *Chasmantha* or *Mecocarpus*. Fries' sections and his phenomenal revision are an excellent tool for that goal because although most of his sections are not natural, many of his species are.

ACKNOWLEDGEMENTS

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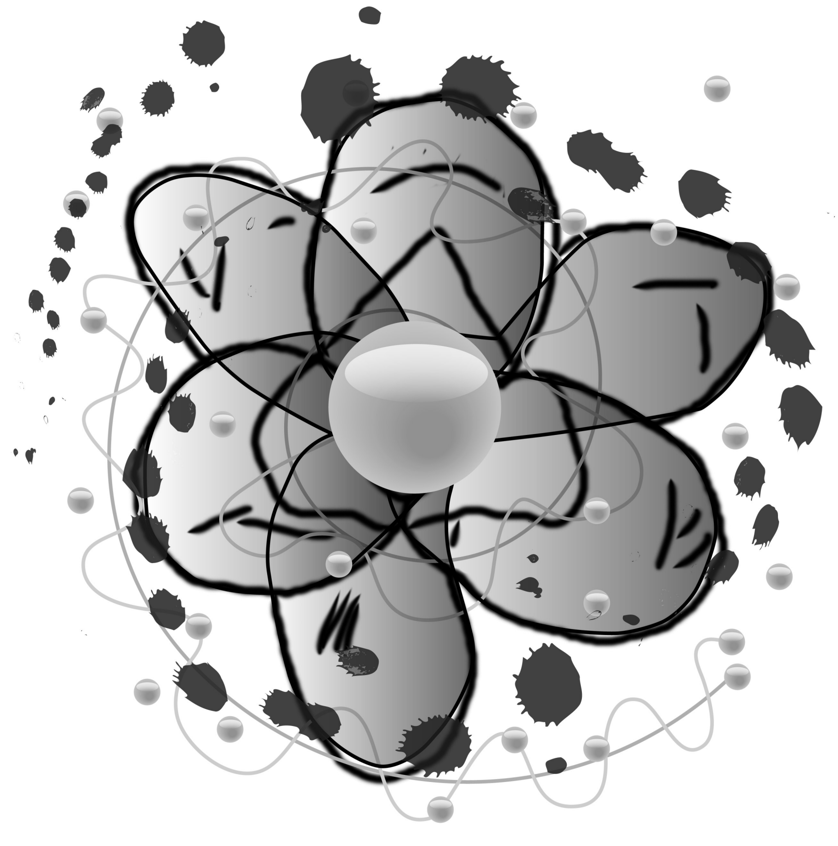

6

TAXONOMIC PROBLEMS IN THE CENTRAL AMERICAN *GUATTERIA AMPLIFOLIA*-COMPLEX (ANNONACEAE) CANNOT BE ELUCIDATED BY AFLP ANALYSES AND SEQUENCE MARKERS

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M. Vrielink-van Ginkel[2] & Paul J. M. Maas[1]

ABSTRACT

Species complexes can prove to be an excellent opportunity to study the patterns of evolution of characters associated with speciation. The *Guatteria amplifolia*-complex (Annonaceae) is the most problematic complex of *Guatteria* species in Central America and can be a model case to study patterns of diversification. The complex has originated after a migration from South into Central America and is thought to consist of three species: *G. amplifolia* Triana & Planch., *G. diospyroides* Baill. and *G. inuncta* R.E.Fr. AFLP markers in conjunction with plastid and nuclear sequence data were used to gain insight into the phylogenetic relationships among *Guatteria*-accessions in the *Guatteria amplifolia*-complex and the pattern of morphological evolution within this complex. *G. inuncta* possibly does not belong to the *Guatteria amplifolia*-complex. The remaining accessions of *G. amplifolia* and *G. diospyroides* together are monophyletic but could not be separated into well differentiated clades on the basis of the molecular data used, with one exception. A specimen that was erroneously identified as *G. amplifolia* on the basis of its leaves with impressed secondary venation proved to be *G. costaricensis*. Because of this, the use of this homoplastic complex-delimiting character is questioned. The fact that it is not possible to differentiate between clades might indicate that the morphological distinction between *G. amplifolia* and *G. diospyroides* is not trustworthy. An alternative explanation for the lack of genetic divergence might be found in the recent common genetic history or ongoing hybridization. For now, it can be concluded that *G. amplifolia* (including *G. diospyroides*) can be seen as an ochlospecies *sensu* White or a complex species *sensu* Pennington because the complex shows considerable morphological variation, that is geographically (and phylogenetically) not well correlated.

Keywords: Species complex, *G. amplifolia*, *G. diospyroides*, *G. inuncta*, morphology

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INTRODUCTION

Relationships among plant groups at higher taxonomic levels have become increasingly clear. A large number of phylogenetic hypotheses for relationships at family and genus level for many different plant groups can be found in the systematic literature. However, so far it has proven difficult to resolve relationships among closely related, recently diverged species or intraspecific taxa (Crawford & Mort, 2004). Resolution of relationships at these levels is of importance because it enables the study of patterns of evolution of characters associated with speciation as opposed to characters that evolved subsequent to divergence (Templeton, 1981). Phylogenies are an essential tool for elucidating these patterns of lineage diversification at species and intraspecific level (Avise, 2000). Species complexes can prove to be an excellent opportunity to study the processes underlying divergence processes because the species may be presumed to be closely related and recently diverged.

The Neotropical tree genus *Guatteria* holds approximately 10% (c. 290 species) of the species in Annonaceae and it is the largest genus in the family. It is distributed throughout the Neotropics from southern Mexico to the south of Brazil. Although the largest genus in Annonaceae, it can be seen as conservative with regard to its morphological evolution in comparison to other large Annonaceae genera such as *Annona* or *Uvaria*. A large number of species can fairly easily be recognised. At the same time quite some species (or rather, names) can at best be grouped into complexes. In the past, species have often been described from different countries and could quite easily be separated geographically. However, with the increased amount of herbarium material collected it has become clear that many of these species show overlap in their morphological characters. Examples of such complexes are the *Guatteria trichoclonia*-complex (distributed throughout the full range of the genus), the *Guatteria schomburgkiana*-complex (occurring in the Guiana shield and Amazon region), and the Central American *Guatteria amplifolia*-complex. The close affinities between the species in these complexes is generally confirmed by phylogenetic analyses (chapter 4 and 5), although some species might be grouped into complexes on the basis of homoplastic characters (e.g. the hairs of the *Guatteria trichoclonia*-complex).

The *Guatteria amplifolia*-complex (GAC) is without any doubt the most problematic complex of *Guatteria* species in Central America. Patterns of variation, i.e. morphologically very similar species, with high variation among populations within a species, resemble those found in other Annonaceae genera in Central America (Murray, 1993; Chatrou, 1997). The complex is thought to have originated after a migration from South into Central America, in conjunction with the closing of the Isthmus of Panama (c. 3.5 million years ago; this thesis, chapter 4). It is thought to consist of four species: *G. amplifolia* Triana & Planch., *G. diospyroides* Baill., *G. inuncta* R.E.Fr. and the poorly known *G. platypetala* R.E.Fr. from Guatemala. The latter species is thought to be a synonym of *G. diospyroides* but it has not been officially synonymised yet. Despite of this, it will be treated here as part of *G. diospyroides*.

G. amplifolia is described from Panama (Fries, 1939) and can be recognised by very large leaves and petioles with the secondary veins distinctly impressed on the upper side; furthermore, the leaf base is obtuse to cordate with the basal margins somewhat inflexed. *G. diospyroides* (including subspecies *diospyroides* and *hondurensis* and *G. platypetala*) can be

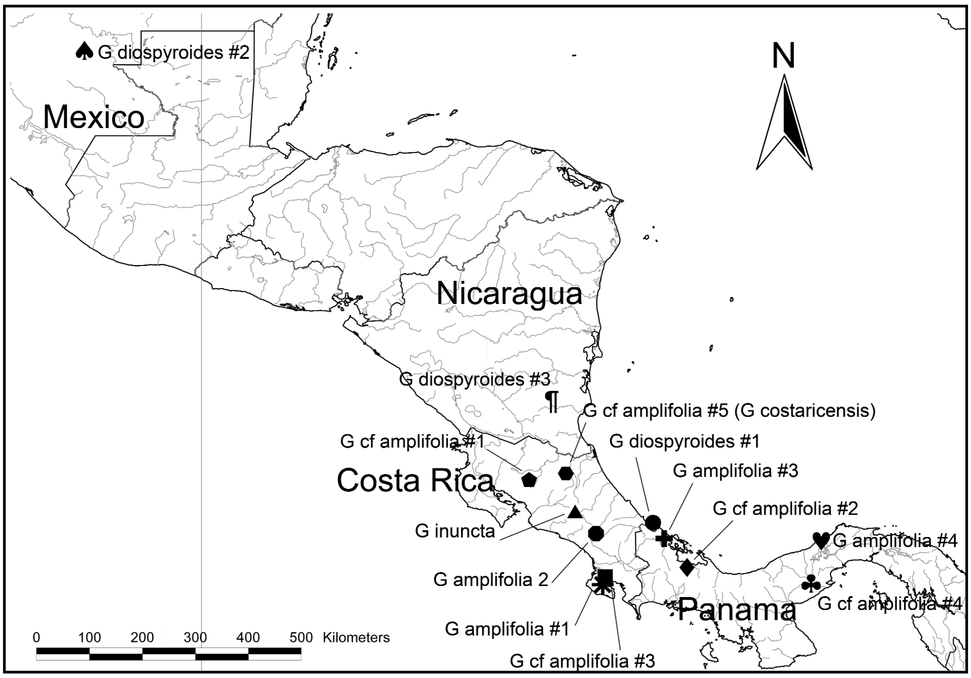

Figure 2. Distribution map of collection sites of 13 specimens from the *Guatteria amplifolia*-complex used in this study.

found from Panama up to Mexico. This species is easily confused with *G. amplifolia* but its leaves are much smaller and it often has three axillary flowers in a single leaf axil (of which only one is persistent; Zamora V. & al., 2000). According to Fries (1939) it is a variable species, which he only knew from Mexico, Guatemala and Belize. He already mentioned some specimens from Honduras and Belize that looked intermediate between *G. diospyroides* and *G. amplifolia* which he placed in *G. diospyroides* subsp. *hondurensis*. Nowadays *G. diospyroides* is thought to be distributed from Panama up to Mexico (Zamora V. & al., 2000).

G. inuncta (including varieties *minor*, *caudata* and *inuncta*) has been described by Fries (1939) as a new species, split off from *G. diospyroides* within Costa Rica and only known from that country. However, he mentions that there are some specimens from Nicaragua that might be identified as *G. inuncta*. In general this species is seen as part of *G. diospyroides*, although it has not been synonimised yet.

The complex as a whole is usually recognised by its distinct impressed secondary venation on the upper side of the leaf, a rare feature that probably only occurs in one other Central American *Guatteria* species (*G.* sp. 2, this thesis chapter 10). Recent morphological work for the Flora Mesoamericana project (this thesis, chapter 10) was unable to separate *G. amplifolia*, *G. diospyroides* and *G. inuncta* from each other. The specimens at the extremes of the distribution were easy to distinguish but many morphological intermediates existed that blurred the division. As these morphological changes were quite gradual they were considered to fall within the variation of one species, namely *G. amplifolia*, which is the oldest name. Furthermore, different morphological forms (e.g. large- and small-leaved trees) seem to occur sympatrically. At the moment, as described for Flora Mesoamericana

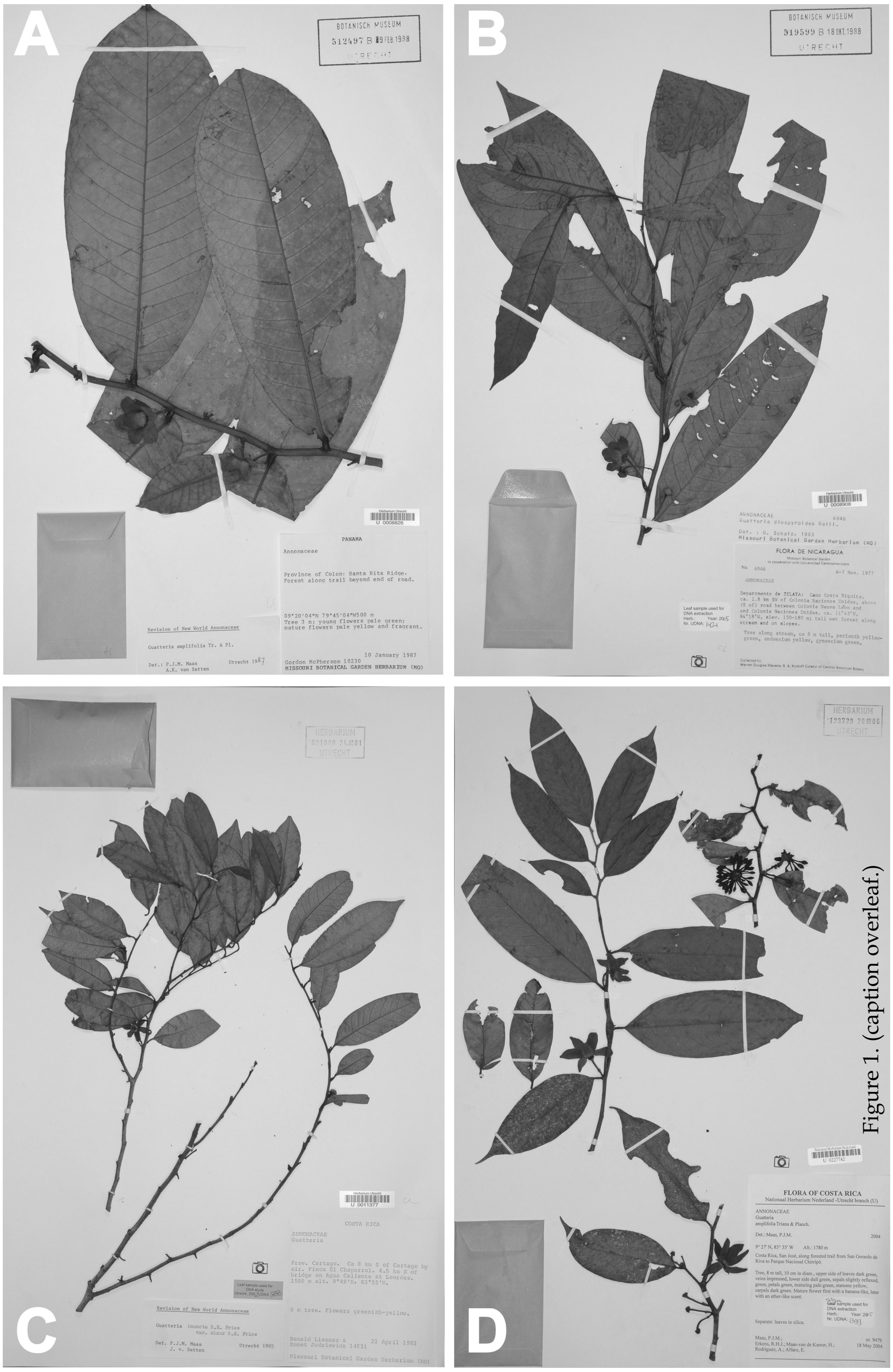

Figure 1. (caption overleaf.)

G. amplifolia is a highly polymorphic, very broadly circumscribed species (figure 1).

In the present study AFLP markers are used in conjunction with plastid and nuclear sequence data to gain insight in the phylogenetic relationships between *Guatteria*-accessions in the GAC. The aims of the study are to find out whether: (1) the three species are phylogenetically distinct and monophyletic, (2) the phylogenetic pattern correlates with morphological characters (i.e. synapomorphies exist for the recovered clades), and (3) the morphological variation correlates to geographical distribution.

MATERIALS AND METHODS

Taxon sampling

This analysis includes 12 (putative) specimens of *Guatteria amplifolia* and *G. diospyroides* and one accession of *G. inuncta* (voucher information in appendix 1; distribution of collections in figure 2). Specimens were dried on silica gel or, when recently collected leaf material was not available, herbarium specimens were used. *G. anomala* and *G. wachenheimii* were included as more distant relatives (chapter 4 and 5) and these species were appointed as outgroups.

DNA extraction, amplification and sequencing

Total genomic DNA from fresh silica-dried leaves and herbarium specimens was extracted using a modified CTAB method (Doyle & Doyle, 1987; this thesis, chapter 7). For all accessions the plastid *psbA-trnH* intergenic spacer was amplified and sequenced with primers psbA and trnH. Low-copy nuclear genes in plants hold a great potential to improve the robustness of phylogenetic reconstruction, especially at low taxonomic levels where universal plastid DNA markers are unable to generate strong phylogenetic hypotheses (Sang, 2002). Therefore, a portion of the low-copy nuclear plastid-expressed glutamine synthetase gene (*ncpGS,* intron 7) was amplified and sequenced with primers GScp687f (Emshwiller & Doyle, 2003) and U1R (5′-CCAGATGTGATCCCCTG-3′).

A standard PCR protocol (35 cycles; 30 sec.: 94°C, 30 sec.: 53°C, 1 min.: 72°C, with an initial 5 min.: 94°C and final 10 min.: 72°C) was used and 0.4% BSA was added to the mixes. PCR products were purified using the QIAquick PCR purification kit (Qiagen) and cycle-sequenced with BIG-DYE terminators (Applied Biosystems) and run on an ABI 3730XL automated DNA sequencer.

AFLP fingerprinting

The AFLP procedure was mainly carried out according to Vos & al. (1995). For the restriction of genomic DNA between 300-500 ng DNA per accession was digested for one hour at 37°C using 5 U (units) *Eco*RI, 5 U *Mse*I, 4 µl 10x restriction buffer and 1 µl BSA in a total volume of 40 µl. Ligation was done for 3 hours at 37°C after addition of 10 µl ligation mixture. This mixture consisted of 1 µl *Eco*RI-biotine adapter, 1 µl *Mse*I adapter, 1 µl 10 mM ATP, 1 µl 10x restriction buffer, 2 U T4 DNA ligase and distilled water. This primary template was diluted 10 times with $T_{0.1}E$ buffer.

Figure 1 (previous page). Morphological variation in the Guatteria amplifolia-complex. A. *Guatteria amplifolia* (*McPherson 10230*; U), B. *Guatteria diospyroides* (*Stevens 4946*; U), C. *Guatteria inuncta* (*Liesner & Judziewicz 14631*; U), D. *Guatteria* cf. *amplifolia* (*Maas & al. 9479*; U).

After adapter ligation, pre-selective amplification was carried out by using 5 µl of the diluted template DNA. The 20 µl reaction mix contained per sample 0.6 µl unlabeled *Eco*-primer (50 ng/ µl), 0.6 µl unlabeled *Mse*-primer, 0.8 µl 5 mM dNTP's, 2 µl 10x buffer 0.08 µl Taq polymerase (5 U/ µl) and 11 µl distilled water. The PCR protocol used consisted of 24 cycles, each with 30 sec. at 94°C, 30 sec. at 56°C and 1 min. at 72°C.

The resulting product was diluted 50 times with $T_{0.1}E$ buffer. Selective amplification was conducted with six IRD 700 labelled primer combinations with three selective nucleotides each: (1) *Mse*I+CAC and *Eco*RI+AAC (M48 – E32), (2) *Mse*I+CAG and *Eco*RI+AAC (M49 – E32), (3) *Mse*I+CAC and *Eco*RI+ACC (M48 – E36), (4) *Mse*I+CAG and *Eco*RI+ACC (M49 – E36), (5) *Mse*I+CAC and *Eco*RI+ACG (M48 – E37), and (6) *Mse*I+CAG and *Eco*RI+ACG (M49 – E37). The reaction mix for these selective amplifications contained 5 µl DNA, 0.3 µl unlabeled *Mse*-primer (50 ng), 0.5 µl labelled *Eco*-primer (1 pmol/ µl), 0.2 µl 10mM dNTP's, 1 µl 10x buffer, 0.04 µl (5 U/ µl) Taq polymerase and 2.8 µl distilled water. The touch-down PCR protocol had an initial 12 cycles with 30 sec. at 94°C, 30 sec. at 65-56°C (0.7°C decrease per cycle), and 1 min. at 72°C. The PCR was continued with and additional 24 cycles, each with 30 sec. at 94°C, 30 sec. at 56°C, and 1 min. at 72°C.

Lastly, selective amplification products were separated on a LI-COR automated sequencer (4300 DNA Analysis System; LI-COR Biotechnology) using a SequaMark 10 bp ladder (LI-COR Biotechnology) as a lane standard.

Data analysis

DNA sequences were edited and assembled in SeqMan 4.0 (DNAStar Inc., Madison, WI) and manually aligned. Indels in the *ncpGS* region were coded using simple gap coding (Simmons & Ochoterena, 2000). AFLP-Quantar® version 1.0 (Keygene Products BV, Wageningen, The Netherlands) was used to score AFLP fragments as present, absent or missing (in cases of doubtful positional homology or low intensity). Both parsimony and Neighbour-Joining (NJ) analyses were conducted. Robust branches are expected to be resolved with both tree-building strategies and can therefore be recognised as such (Koopman & al., 2001). However, the partitions were also tested for incongruence using the incongruence length difference test (Farris & al., 1995) as implemented in PAUP*, with 100 replicates and 10 additional sequence replicates with equal weights and TBR swapping.

Most-parsimonious trees were generated from 10,000 replicates of random taxon addition and swapped using tree bisection-reconnection (TBR), equal weights and a maximum of 10 trees held at each step, using PAUP* 4.0b10 (Swofford, 2003). Bootstrap analysis (Felsenstein, 1985) with 10,000 replicates and 10 additional sequence replicates was performed with equal weights and TBR swapping, saving a maximum of 10 trees for each replicate. Bootstrap support of 50–74% is considered to represent weak support, 75–89% moderate support and 90–100% strong support.

The results obtained from the AFLP procedure were analysed with NTSYS-PC (Rohlf, 2005). The Dice similarity coefficient (Dice, 1945) in combination with the NJ method (Saitou & Nei, 1987) was applied to generate phenograms. Distance calculations based on Dice's similarity coefficient (comparable to Nei and Li's (1979) coefficient) are more reliable because only shared bands are scored, thus avoiding the issue of joint band absence being considered a homologous character state. NJ bootstrapped phenograms were calculated with 10,000 replicates.

To test for correspondence between the data of the six primer combinations, Dice similarity matrices were constructed for each primer combination separately and a two way Mantel test (standardised Mantel statistic *r*) was used to compute pairwise correlations among them. One-tailed test statistic probabilities were obtained through 10,000 permutations. Furthermore, a similar Mantel test was conducted for correlation between genetic distance and geographical distance. For this purpose, a geographical distance matrix was constructed based on the coordinates or the collection site information on the vouchers labels.

RESULTS

ncpGS and psbA-trnH sequence data

From all accessions *ncpGS* and *psbA-trnH* sequences were obtained. The *ncpGS* alignment was 682 bp long and contained 37 parsimony informative characters and 6 parsimony informative indels. The exons flanking intron 7 are highly conserved and could easily be aligned with the homologous exons in *Oxalis* (Oxalidaceae) on which the primers were originally designed. A quick survey of this region for amplification success in Annonaceae as a whole resulted in intron lengths between 300 (*Duguetia*) and 600 bp (*Guatteria*), whereas in *Oxalis* it was only 96 bp. The intron was found to be very AT-rich (up to c. 70%).

Phylogenetic analysis of the *ncpGS* sequences yielded 101 most parsimonious trees with a length of 82 steps, a consistency index (CI) of 0.93 and a retention index (RI) of 0.90. Bootstrap analysis strongly supports *Guatteria inuncta* as sister to a clade containing all *G. amplifolia* and *G. diospyroides* accessions (bootstrap support (BS) 98%; figure 3A). This clade, the GAC without *G. inuncta*, will from here on be referred to as *G. amplifolia* s.l. Not much phylogenetic structure is present within in the latter clade. The sistergroup relationship of *G. diospyroides* accessions #2 and #3 from Mexico and Nicaragua receives strong bootstrap support (BS 95%) and a clade consisting of accessions from Panama and the Osa region in southeast Costa Rica is weakly supported (BS 64%). The specimens from the Osa Peninsula together also form a weakly supported clade (BS 63%). The position of *G.* cf. *amplifolia* #5 is surprising because it is placed within the outgroup as closest relative to *G. wachenheimii* (BS 86%).

A single most parsimonious tree resulted from phylogenetic analysis of the *psbA-trnH* region, with a length of 17 steps (CI 1.0; RI 1.0; figure 3B). Although *psbA-trnH* has so far proven to be the one of the most variable plastid marker within Annonaceae (Pirie & al., 2006), it only contains six parsimony informative characters in this analysis. All species in the GAC form a weakly supported clade (BS 63%), as well as a clade containing two accessions from the Costa Rican Osa Peninsula and San José region, respectively (BS 63%). All accessions from Panama together with *G. inuncta* and one *G. diospyroides* collection from the Limón region in Costa Rica comprise another weakly supported clade (BS 64%). The two specimens from eastern Panama comprise another weakly supported clade (BS (63%). In contrast to the nuclear analysis, in the plastid analysis *G. inuncta* is nested within the GAC instead of sister to it but support for this topology is very weak. Again *G.* cf. *amplifolia* #5 is placed within the outgroup.

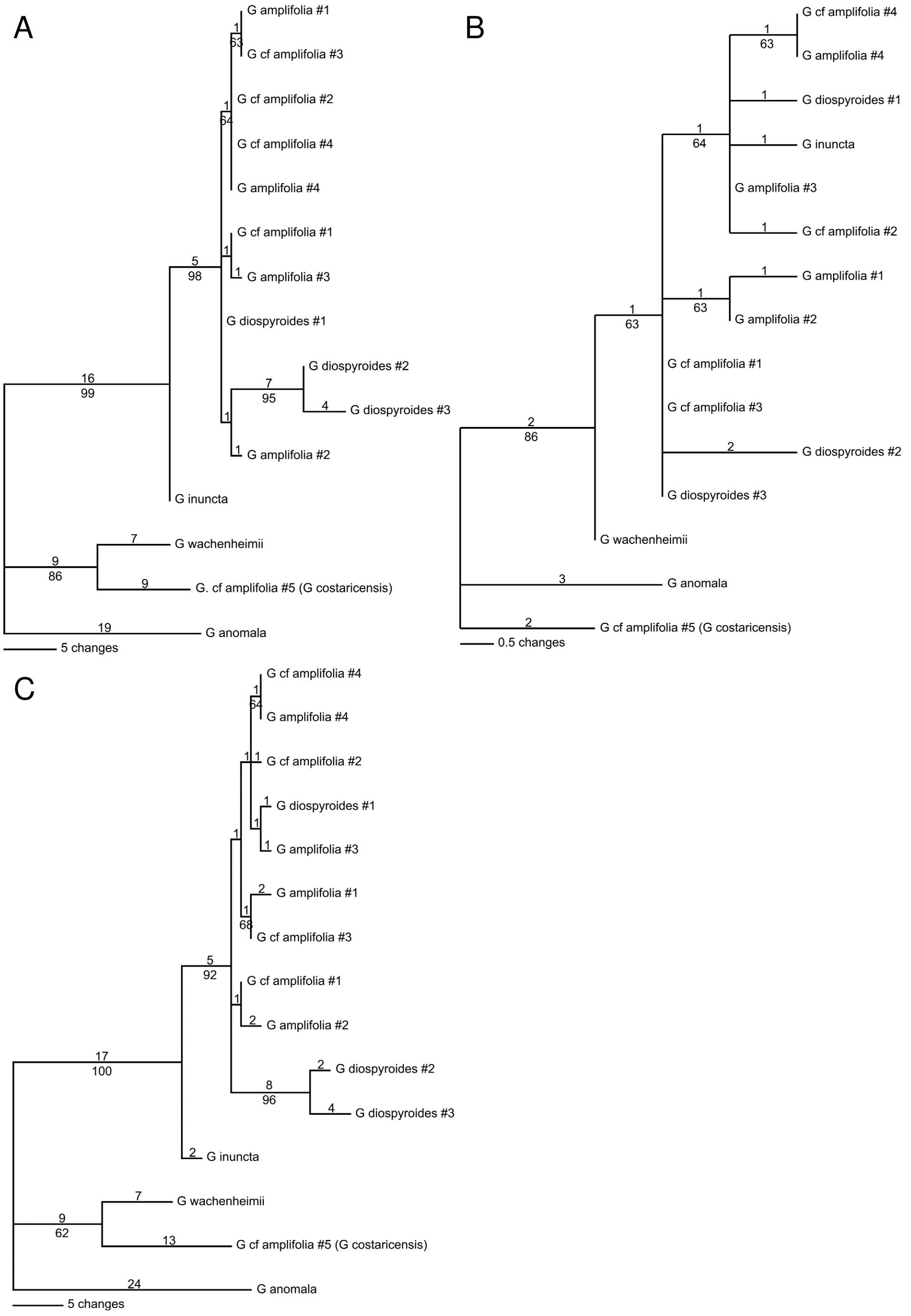

Figure 3. A. Phylogram of one of 101 most parsimonious *ncpGS* trees, B. Phylogram of the single most parsimonious *psbA-trnH* tree, C. Phylogram of one of 103 most parsimonious trees of the combined analysis of *ncpGS* and *psbA-trnH*. Branch lengths are indicated above the braches, bootstrap values below.

Table 1. Mantel test statistics (r) based on Dice similarity matrices (0.9 <= r indicates very good fit; 0.8 <= r < 0.9: good fit; 0.7 <= r < 0.8: poor fit; and r < 0.7: very poor fit). All values are significant (one tailed P<0.005) after 10.000 permutations. Numbers indicate primer pair combinations: (1) M48 - E32, (2) M49 - E32, (3) M48 - E36, (4) M49 - E36, (5) M48 - E37, and (6) M49 - E37.

	1	2	3	4	5	6
1	-					
2	0.796	-				
3	0.916	0.766	-			
4	0.935	0.799	0.965	-		
5	0.818	0.750	0.872	0.868	-	
6	0.843	0.828	0.901	0.890	0.918	-

The ILD test showed no incongruence between the nuclear and plastid region (*p*=0.09). Also visual inspection for incongruencies revealed no moderately or strongly supported incongruent clades (figure 3A and 3B). Therefore, both partitions were combined in a single phylogenetic analysis. This analysis resulted in 103 most parsimonious trees of 104 steps (CI 0.89; RI 0.85; figure 3C). *Guatteria inuncta* is strongly supported (BS 92%) as sister to *G. amplifolia* s.l. Not all relationships between accessions of *G. amplifolia* s.l. are resolved. Nevertheless, three clades can be identified. There is strong support for the grouping of two *G. diospyroides* accessions from Mexico and Nicaragua (BS 96%). Furthermore, two specimens from eastern Panama form a weakly supported clade (BS 64%) as well as the two species from the Costa Rican Osa Peninsula and San José region (BS 68%). Within the outgroup, *G.* cf. *amplifolia* #5 is placed as sister to *G. wachenheimii* (BS 62%). All BS values in the ingroup (except for the node supporting the sistergroup relation of *G. inuncta*) are higher than in the separate analyses.

AFLP analysis

The six AFLP primer combinations yielded 199 unambiguously scorable polymorphic bands. AFLP fragment sizes ranged from approximately 50 to 450 bp. Polymorphic fragments were distributed across this entire range with the major proportion present between 100 and 300 bp. A correlation test performed on each pairwise combination of six Dice similarity matrices, obtained from analysis of each primer combination, revealed that most combinations exhibited good to very good fit (table 1). An exception is primer combination (2) that correlates poorly with the information of the other combinations. All values are significant (one tailed *P*<0.005) after 10,000 permutations. Analysing the data with parsimony and NJ but without primer combination (2) resulted in congruent but less resolved trees than obtained on the basis of all AFLP markers combined. Apparently, aberrant primer combination (2) did contribute to the phylogenetic signal. In addition, the ILD test did not indicate any incongruence between the different AFLP data partitions (*p*=0.16). All AFLP data were pooled for further analysis and only this combined analysis will be discussed here.

The NJ phenogram (figure 4) shows that the GAC is a well supported group (BS 100%) and that *G. inuncta* is sister to *G. amplifolia* s.l. (BS 72%). Furthermore, two Costa Rican accessions together (BS 65%) are sister to a weakly supported group (BS 69%) that contains two Costa Rican accessions and all non-Costa Rican collections. The specimens from Mexico and Nicaragua from a group (BS 76%), as well as an accession from the Osa Peninsula and San José region in Costa Rica (BS 89%), two specimens from central Panama (BS 100%), and lastly two specimens from central Panama (BS 76%). *G.* cf. *amplifolia* #5 is placed with *G. anomala* at the base of the tree.

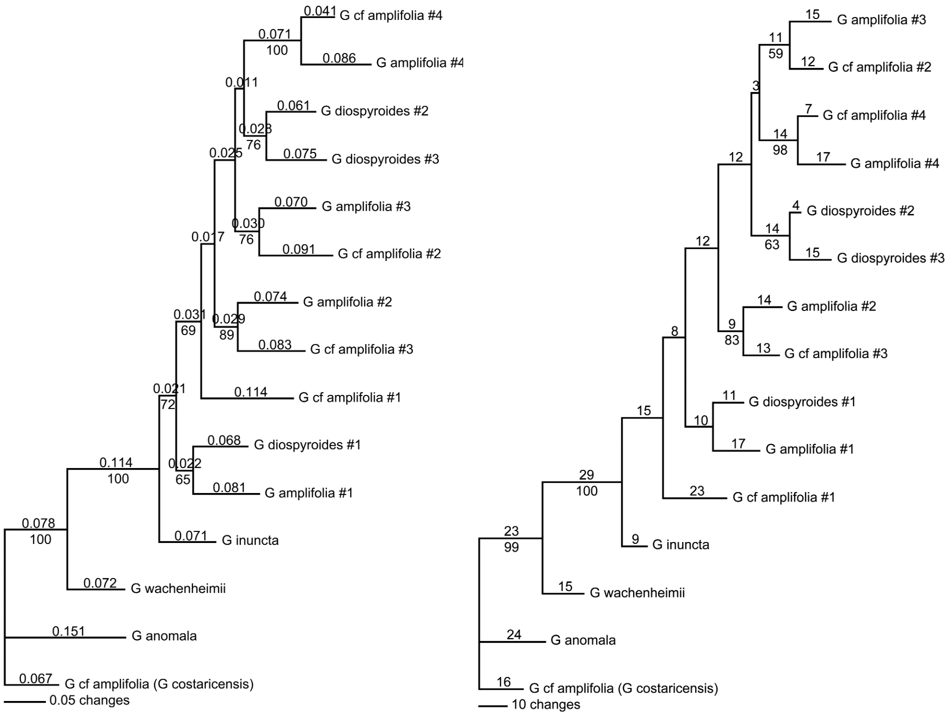

Figure 4. Neighbour-Joining (left) and one of four most parsimonious AFLP trees (right) combined. Branch lengths are indicated above the braches, NJ and parsimony bootstrap values below respectively.

Phylogenetic analysis of the complete AFLP data set resulted in four most parsimonious trees of 372 steps (CI 0.53; RI 0.53; figure 4). Supported relationships and BS values are comparable to the NJ tree. The placement of *G. inuncta* as sister to *G. amplifolia* s.l. is identical in both topologies, but is not supported by bootstrap support in the cladistic analysis.

Combined analysis of nuclear, plastid and AFLP data

No incongruence was found between the data partitions containing sequence data or between the different AFLP data partitions (see above). The ILD test was also non-significant for the sequence data versus the AFLP data partitions (p=0.92), indicating that there is no significant conflict between the partitions. Indeed, no major topological incongruencies exist between the analyses based on different data partitions (figure 3 and 4). Therefore, phylogenetic analysis of the total data set was carried out, which resulted in two most parsimonious trees of 482 steps (CI 0.60; RI 0.57; figure 5).

G. cf. *amplifolia* #5 is placed near the root of the tree together with *G. anomala* and this position is strongly supported. The position of *Guatteria inuncta* as sister to *G. amplifolia* s.l. is also strongly supported (BS 90%). One larger weakly supported clade can be found in the GAC (BS 53%), itself containing a clade with an accession from the Osa Peninsula and San José region in Costa Rica (BS 73%), a clade with specimens from Mexico and Nicaragua (BS 97%), a clade with two specimens from central Panama (BS 99%), and lastly two specimens from western Panama (BS 52%). The relationships between these clades are unresolved.

Geographical patterns

Correlation between absolute sequence divergence and geographical distance was investigated using a Mantel test. No correlation was found between *ncpGS* or *psbA-trnH* sequence divergence and the geographical distances between the different accessions (*ncpGS*: $r= 0.072$, $p= 0.214$; *psbA-trnH*: $r= 0.211$, $p= 0.255$). Furthermore, the Mantel test revealed no correlation among AFLP data and geographical distances between the different accessions of the GAC when all markers were analysed separately ($-0.183 < r < 0.321$, $0.094 < p < 0.790$) or together ($r=0.102$, $p=0.214$). Therefore, we can conclude that for none of the data partitions a correlation between sequence divergence and geographical distance exists, i.e. genetically more divergent accessions do not occur at greater distance from each other.

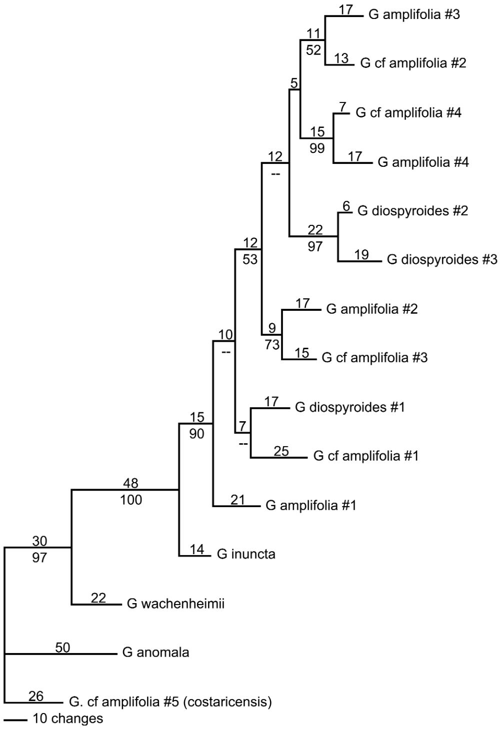

Figure 5. Phylogram of one out of two most parsimonious trees when nuclear, plastid and AFLP data are combined. Branch lengths are indicated above the braches, bootstrap values below.

DISCUSSION

Marker utility

In this study the nuclear *ncpGS* region was used together with the *psbA-trnH* plastid region because the phylogenetic utility of plastid DNA is largely limited by its slow rates of evolution and uniparental inheritance (Olmstead & Palmer, 1994). This is confirmed here by the fact that the *psbA-trnH* region, one of the most variable cpDNA markers within Annonaceae, proved quite useless to reconstruct relationships on the (intra-)specific level. In contrast, intron 7 of the nuclear *ncpGS* region proved to be more informative, as indicated by a fivefold difference in tree length after separate analysis of the two markers, and a higher number of strongly supported nodes in the *ncpGS* tree. The intron was reported to be 96 bp long in *Oxalis* (Emshwiller & Doyle, 2003) but was found to be much longer in *Guatteria* (c. 600 bp). Furthermore, it seems to be very AT-rich, up to c. 70% of the intron consisted of one of these two bases. These are typical values for plants, which usually have higher AT content in the introns than in the surrounding exons (Goodall & Filipowicz, 1989; Csank & al., 1990). However, it is interesting to note that the A : T ratio for this region in *Guatteria* is c. 1.7 : 1 instead of the average 1 : 1.45 for dicots (Goodall & Filipowicz, 1989).

AFLP and sequence data congruency

The drawback of gene sequence data is that phylogenetic analysis results in a gene tree that does not necessarily reflect the true species tree. The simultaneous analysis of many loci representing the whole genome (such as AFLP data) has the potential to generate a true species tree, especially among closely related, potentially interbreeding species where reticulate evolution may occur (Després & al., 2003). There are however several general theoretical drawbacks to the use of AFLP data in a cladistic framework, such as possible non-homology, non-independence of bands, unequal gain/loss probability and no distinction of heterozygotes (dominant scoring only). However, it has been shown that the presence of phylogenetic signal in AFLP data sets does warrant cladistic analyses (Koopman, 2005).

Information from one of the AFLP primer combinations correlated poorly with the information of the other combinations (although no conflict was detected by the ILD-test). However, the use of this aberrant primer combination resulted in better resolution and increased support. It has already been shown that simultaneous ("total evidence") analysis of data partitions can allow hidden signals to emerge because it measures strength of evidence supporting disparate results (Nixon & Carpenter, 1996). In separate datasets common character support for these emergent relationships is hidden by conflicting characters (Gatesy & al., 1999). In order to understand the differences among data partitions separate analyses are useful, but simultaneous analysis provides the greatest possible explanatory power (Nixon & Carpenter, 1996). A total evidence approach should therefore always be carried out, regardless of results of tests as the ILD-test.

No strongly supported topological difference was found between the phenetic and cladistic analysis of the AFLP data (figure 5). Furthermore, when comparing branch support and topological congruence between the cladistic analyses of the sequence and AFLP data it was found that the well supported parts of the trees show similar relationships, while the differences in the remaining parts of the trees are not or only poorly supported (figures 3-5). This yet again demonstrates the presence of phylogenetic signal in AFLP data and corroborates the idea of combining AFLP data with sequence data as was done or suggested in previous studies (e.g. Després & al., 2003; Pelser & al., 2003; Crawford & Mort, 2004; Koopman, 2005).

Phylogenetic relationships

G. cf. *amplifolia* #5 was placed in all analyses within the outgroup and this position always had strong support. The position of *G. inuncta* as sister to the remaining species of the GAC is also strongly supported. Furthermore, two clades within *G. amplifolia* s.l. are strongly supported in this study. These clades contain specimens from the extremes of the distribution of the complex. One clade contains specimens from Mexico and Nicaragua and the other clade specimens from central Panama. The tree in figures 5 does not show any support for the relationships between these species pairs.

The position of *G.* cf. *amplifolia* #5 was surprising. Close morphological re-examination and additional sequencing showed that this accession was wrongly identified as *G.* cf. *amplifolia*. Instead it belongs to *G. costaricensis*, a species placed in the so called Central American

Clade (CAC; chapter 4 and 5) of *Guatteria*. The species in this CAC are not at all related to the species in the GAC (this thesis, chapter 4 and 5). The erroneous placement of both this accession and of *G. inuncta* (see below) in the GAC illustrates the non-functionality of the impressed secondary venation as a trustworthy (field) character. This character seems homoplastic and might be compared to the hairs of the *G. trichoclonia*-complex, another homoplastic complex-delimiting character that should be discarded (this thesis, chapter 8).

Further sequence work also showed that the accession of *G. inuncta* used here, is not at all closely related to the species of *G. amplifolia* s.l. (chapter 4 and 5). In these analyses it is sister to *G. jefensis* (BS 80%), a Central American species from Cerro Jéfe in Panama. If this accession is a good representative of *G. inuncta*, it should not be included in the GAC. More *G. inuncta* accessions should be analysed to corroborate this finding and to allow for definitive conclusions on the in- or exclusion of this species in the GAC.

It seems that *G. amplifolia* and *G. diospyroides* are not worth further recognition. *G. amplifolia* s.l. could not be separated into well differentiated clades that represent these species. This could mean that the (morphological) distinction made between these species is not trustworthy. On the other hand, this pattern could also result from the fact that these two species share a very recent common genetic history (this thesis, chapter 4), leading to a lack of parsimony informative characters and absence of resolution in the tree. This would indicate that most AFLP polymorphisms found are not species-specific, i.e. that ancestral polymorphisms are retained in derived lineages (Després & al., 2003). The recent dispersal of the ancestors of the GAC from South into Central America (c. 2 my ago; chapter 4) and their following (rapid) range expansion was in that case not accompanied by significant genetic diversification.

A third explanation could be that this low resolution is the result of gene flow occurring between previously isolated and well separated species in geographically adjacent areas (Després & al., 2003). Gene flow can probably occur if *G. amplifolia* and *G. diospyroides* share the same pollinator. Nearly all species of *Guatteria* that have been studied so far are uniform with respect to flower biology and are pollinated by fruit-eating Nitidulidae (small beetles; Gottsberger, 1999) or Staphilinidae (Webber, 2002). This uniformity and the fact that beetles are very indiscriminate with regard to which plants they pollinate increases the chance of cross-pollination. This was shown by recent findings in *Polyalthia* where the same beetle functioned as the primary pollinator of different *Polyalthia* species (Ratnayake & al., 2006). The same beetles were also observed to pollinate species of *Goniothalamus*, another Annonaceae genus. This indicates the ease with which beetle cross-pollination might be achieved between species and even between genera. Extrapolating these results to *Guatteria*, which has a comparable pollination syndrome, leaves open the possibility of gene flow and hybridization, resulting in a homogenous genetic structure.

The latter hypothesis is reinforced by the fact that the strongly supported clades in figure 5 are specimens from the extremes of the distribution. Especially the relationships between the specimens from Costa Rica and western Panama (the geographical centre of distribution of the complex) are unresolved. The longer branches leading to the strongly supported clades might indicate less genetic homogenisation.

Morphological evolution

Several species pairs always recur in the analyses based on different data partitions. *G. diospyroides* #2 and #3 (from Mexico and Nicaragua) mostly form a clade. Both accessions show the typical thickened *G. amplifolia* petiole but the base of their leaves is acute rather than cordate. In general, they both seem to fit the circumscription of *G. diospyroides* sensu Baill. well.

The two specimens from central Panama are morphologically very dissimilar. *G. amplifolia* #4 has large leaves with an impressed venation, a thick petiole and a stem-clasping leaf base. Furthermore, this specimen has an old calyx present around its pedicels (a feature observed with more specimens in the field in Panama – personal observation). This specimen is without a doubt *G. amplifolia* as described by Triana and Planchon. However, *G.* cf. *amplifolia* #4 has the impressed venation and thickened petiole characteristic of *G. amplifolia*, but its leaves are much smaller, has longer pedicels (up to 35 mm, rare in *Guatteria*) and a slight zigzag pattern in its younger branches.

The two specimens from western Panama show the same pattern as the Central Panamanian specimens. *G. amplifolia* #3 has the typical large leaves with impressed venation and a thick petiole (and a slight zigzag pattern in its young branches), while *G.* cf. *amplifolia* #2 is much smaller in its features, has an acute leaf base and a thinner petiole (looking more like *G. diospyroides*).

The conflict between the different phylogenetic analyses always centres around several specimens from Costa Rica. Surprisingly, these are morphologically more uniform than the accessions from the supported clades mentioned above. *G. amplifolia* #1, *G. amplifolia* #2, *G.* cf. *amplifolia* #1, and *G. diospyroides* #1 all have large leaves with impressed secondary venation, a thickened petiole and a more or less cordate leaf base. *G. amplifolia* #2 additionally has multiple axillary flowers per single leaf axil and somewhat longer pedicels than the other specimens (up to 25-30 mm). All these specimens fall within the circumscription of *G. amplifolia* sensu Triana and Planch.

The only morphologically aberrant specimen is *G.* cf. *amplifolia* #3. It has young twigs that are more hairy and show a zigzag pattern (a rare feature for *G. amplifolia*), a flat to slightly raised secondary venation upon drying and multiple axillary flowers. With respect to the hairiness it bears resemblance to *G. dolichopoda* (a species from another Central American species complex: the *Guatteria dolichopoda*-complex). However, the characterising feature of *G. dolichopoda* is a long pedicel of 30-60 mm (exceptionally long for species of *Guatteria*) and this specimen has pedicels of up to 20 mm. The zigzag pattern in combination with erect hairs is known from the Central American species *G. oliviformis* (a species easily confused with *G. costaricensis*). However, *G. oliviformis* also has verrucose leaves and shortly stipitate, thick-walled monocarps. The latter characteristics are not shared with *G.* cf. *amplifolia* #3. The last possible affinity might be with *G. tomentosa* (of the *Guatteria trichoclonia*-complex) due to the hairy twigs but *G. tomentosa* has much larger sepals and is much more hairy than this specimen.

Interestingly, *G.* cf. *amplifolia* #3 resembles other species of *Guatteria* that are themselves part of species complexes. It might therefore be true that species from all these complexes are able to hybridise and that this is the primary cause for the existence of these complexes. Unfortunately, no evidence yet exists to support this claim.

It is clear that the morphological patterns of variation of the studied clades are complex when linked to the phylogenetic patterns found. So far, this makes it extremely difficult to group the accessions into valid taxonomic subdivisions let alone species. Furthermore, if it can be shown that *G. amplifolia* and *G. diospyroides* are able to hybridise (i.e. are indeed genetically non-separated lineages) one should question the idea that *G. amplifolia* and *G. diospyroides* are evolutionary independent lineages. Consequently, they should not be regarded as separate taxonomic species.

CONCLUSIONS

As efforts continue toward elucidating relationships among recently diverged lineages, there will be continued discussion and debate of suitable sources of data and the most appropriate methods of data analyses. These are important issues because resolution of relationships at these lower taxonomic levels is a necessary prerequisite for studying the processes involved in divergence and speciation (Crawford & Mort, 2004). Here the *Guatteria amplifolia*-complex was used as a model taxon to study lineage diversification at (infra)specific level. It is found that *G. inuncta* might not belong to the GAC and that an accession of *G. amplifolia* was erroneously put into the complex on the basis of its impressed leaf venation (a possible homoplastic character). The remainder of the complex proves to be monophyletic but no clearly separated lineages exist within it. The fact that the data presented here are not able to differentiate between clades might indicate a recent common genetic history of all accessions or ongoing hybridization. Furthermore, with regard to morphological evolution it can be concluded that *G. amplifolia* s.l. shows considerable morphological variation and that this variation is geographically not well correlated. This pattern is also found in the genetic data: no correlation between absolute sequence divergence and geographical distance exists. Therefore, *G. amplifolia* s.l. might be seen as an "ochlospecies" *sensu* White (White, 1962) or a complex species *sensu* Pennington (Pennington, 1981).

More accessions of the putative species in the GAC (especially *G. diospyroides* and *G. inuncta*) are necessary to gain better insight in the phylogenetic relationships and morphological patterns within the GAC. Only then will it be possible to pinpoint characters important for divergence and speciation in *Guatteria*.

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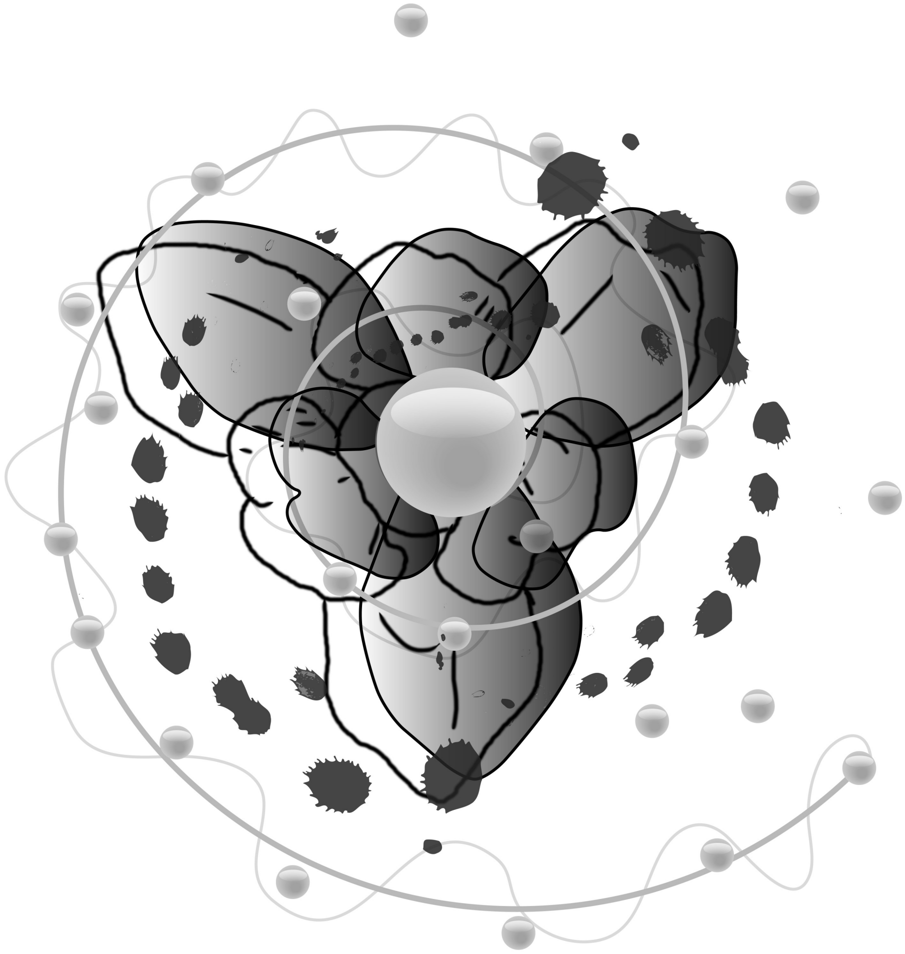

7 REVIEWING ASSUMPTIONS: ASSESSMENT OF AGE AND GREENNESS OF HERBARIUM SPECIMENS AS PREDICTOR FOR SUCCESSFUL EXTRACTION AND AMPLIFICATION OF DNA

Roy H. J. Erkens, Hugh Cross[2], Jan W. Maas[1],
Kim Hoenselaar[3] & Lars W. Chatrou[4]

ABSTRACT

Age and the greenness of leaves have been traditionally used as indicators for selecting herbarium specimens for molecular studies. Although plant DNA extraction and amplification have been common lab procedures for the past 20 years, no studies specifically investigated the success of these indicators. Here the predictive value of age and the greenness for extraction and amplification success is quantitatively assessed, using a large number of herbarium specimens from different plant groups and ranging widely in age and condition. The investigation of these indicators is important because herbarium material is a precious commodity, and is often the only remaining floral record of now extinct ecosystems. In cases where little leaf material is available, most researches still attempt to extract DNA. This study shows that age and greenness of leaves are labile indicators of extraction and amplification success, although taken together can have limited usefulness. Therefore, researchers sometimes should refrain from using rare specimens because chances of success are unpredictable and precious herbarium material might be wasted. The uncritical use of axiomatic indicators such as age or leaf colour is therefore not recommendable. Furthermore, botanists should annotate how specimens were collected and dried because this information is essential for successful DNA extraction. In addition, extraction success, specific extraction methods, PCR protocols etc. should be reported especially when using herbarium specimens. Lastly, the nature of the extracted DNA is of importance and the use of specific and internal primers should be encouraged to amplify (fragmented) DNA regions.

Keywords: laboratory practice, herbarium specimen selection, *Guatteria*, *Zehneria*, Rauwolf

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INTRODUCTION

The use of plant ancient DNA has been steadily growing. The term 'ancient DNA' has been defined as the retrieval of nucleic acids from older organic tissues, including museum collections, archaeological specimens, fossil remains, and many other older and unusual sources of DNA (Pääbo & al., 2004). Herbarium specimens are a commonly sought source of DNA for plant studies. However, before the present era of molecular biology herbarium specimens were never collected with the intention to use the material for DNA extraction, and were therefore often not dried under optimal conditions for preservation of the nucleic acids. This is especially true for tropical specimens that were collected in humid conditions, deep in the forest, with no drying equipment at hand. As a consequence, the DNA molecules in these specimens are more susceptible to degradation by enzymes, bacteria, fungi, and insects that feed on macromolecules (Eglinton & al., 1991). Because of this degradation several studies have been conducted to determine which method of DNA extraction is most suitable for herbarium specimens (Rogers & Bendich, 1985; Savolainen & al., 1995; Drábková & al., 2002; Jankowiak & al., 2005). These studies generally involved a small number of specimens (< 50) and tested which of several extraction methods yielded the highest amount of DNA for these specimens. Although plant DNA extraction and amplification of museum specimens have been common lab procedures for the past 20 years, no reports exist of the extraction and amplification success of a single method used for a large amount of material. Usually, only successful extractions and subsequent amplifications are reported (via for instance a Genbank number), few researchers report on the success rate of their extraction and amplification efforts. Nonetheless, data of the success rate to extract or amplify DNA from certain specimens can be very informative for researchers who need to use (often rare) museum collections for molecular research, in order to develop criteria for selecting the best specimens.

When selecting herbarium specimens for extraction of DNA, researchers often use certain indicators such as age and greenness of the leaves, to assess the likelihood of obtaining DNA of sufficient quantity and quality. The greenness of the leaf is thought to represent the method of drying (Jankowiak & al., 2005). The assumption being that when a specimen was for instance slowly dried (i.e. low heat) it remained green, whereas a quickly dried leaf (i.e. with a lot of heat) turned brown. Jankowiak & al. (2005) recently reported success in extracting DNA from a 100 year-old herbarium specimen of the liverwort *Bazzania triloba* (Lepidoziaceae). They found in their study of 18 samples that the method of drying (as indicated by the colour of the leaves) was more important for isolation of DNA than the age of the sample. These results are in agreement with earlier studies on the effects of different protocols for DNA extraction such as the extraction from 18 herbarium specimens of Juncaceae (Drábková & al., 2002). However, the colour of leaves can be affected by other factors, such as the widely used storage in alcohol prior to drying (Blanco & al., 2006), and can vary from family to family and even from one species to another. For instance, de Wilde and Duyfjes (2006) used the colour of the leaf after drying as a character to distinguish between closely related species of Cucurbitaceae.

The comparison of extraction and amplification results from evolutionary unrelated plant groups from different geographic regions might contribute to our understanding of the usefulness of age and greenness of the leaves as guidelines for selecting herbarium specimens. In this study results from three such groups are compared.

The first study is a recent molecular phylogenetic study of the large Neotropical tree genus *Guatteria* (Annonaceae; Magnoliales, "magnoliids"). Here it was necessary to use many herbarium specimens. The genus has a wide distributional range, from Mexico to South Brazil, and consists of approximately 265 species (Chatrou & al., 2004). Therefore, for many species it was very difficult to obtain freshly collected, silica-dried, leaf material for DNA extraction. Furthermore, the genus has little morphological variation and harbours several species complexes. This made it difficult to assign correct names to some recently collected specimens. In the case of *Guatteria* several type specimens, undoubtedly belonging to such complexes, were sequenced in order to determine the closest affinity of unidentified specimens.

For comparison, a second recent molecular systematic study that utilized many herbarium specimens of several genera in the family Cucurbitaceae (Cucurbitales, "eurosids I") is also considered. The genera under study, primarily *Zehneria* and *Melothria*, but including several others, are found throughout tropical Africa, America, mainland Asia, Indonesia and the Pacific. Because of this broad range and difficulties in obtaining fresh material from throughout the study sites, it was necessary to use herbarium material.

The third study that is compared consists of data of an additional eight specimens from ongoing research on the historic Rauwolf collection at the Leiden herbarium (L). These specimens were collected in the Middle East and date to the 1500's, but are in generally good condition. Specimens representing several plant families (e.g. Poaceae (Poales, "monocots"), Solanaceae (Solonales, "eusasterids I")) were sampled.

Although plant DNA protocols have been around for over 20 years, an evaluation of these procedures has not been published so far. Many researchers use a "modified CTAB method" but the (successful) modifications are usually not reported and stay confined to the laboratory of that researcher. However, insight in successful methods and procedures will be of importance for many researchers who must select among a very few, precious specimens for their studies. Like any museum collection, plant specimens are a valuable resource that should not be squandered. A dialogue among researchers as to the best methods, and reports of the failures as well as the successes, can help avoid the errors of our predecessors. This will prevent more irreplaceable herbarium material ending up at the bottom of a laboratory trash bin.

That the age and greenness of the leaves can serve as guidelines for selecting herbarium specimens is a common assumption, but assumptions may not be a sound basis for laboratory practice. This study takes a quantitative approach to test these propositions. It assesses if age and greenness of herbarium specimens are as good predictors for successful extraction and amplification of DNA as is generally thought. Hopefully, this study serves as a much-needed beginning of a discussion on the use of herbarium specimens for molecular research.

MATERIALS AND METHODS

Herbarium specimen sampling

151 Herbarium specimens from the *Guatteria* study (voucher information in table 3) were used in this study, 78 specimens from the National Herbarium of the Netherlands – Utrecht

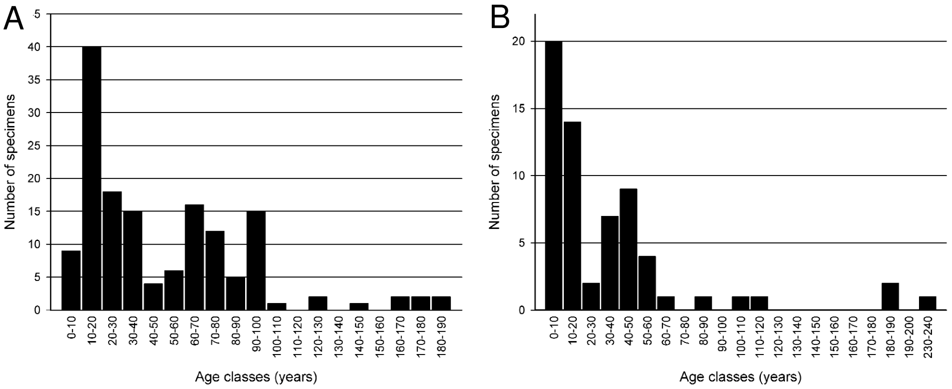

Figure 1. Age distribution of specimens used in this study A. *Guatteria* study and B. *Zehneria* study. Complete voucher information and base data in tables 3 & 4.

branch (U), 9 from the Herbarium of the Royal Botanic Gardens, Kew (K) and 64 type specimens from the Herbarium of the Swedish Museum of Natural History (S). The specimens ranged in absolute age from six to 184 years old (figure 1A). For each specimen the greenness of the leaves was qualified by eye as green, green/brown or brown. From the *Zehneria* study, 64 herbarium specimens were evaluated (voucher information in table 4). Of these, 53 were from the Leiden Branch of the National Herbarium of the Netherlands (L), and 11from the Wageningen Branch (WAG). The specimens from this study ranged in age from three to 240 years (figure 1B). Finally, eight specimens were made available for extraction from the Rauwolf herbarium at Leiden. These were selected to represent several plant groups (table 1).

DNA extraction and purification

All specimens in all studies were extracted according to the protocols described below for each study. The results reported here are always first extraction and amplification efforts (subsequent success for an initial failure, using other techniques or optimizations are not included).

The description of methods might seem elaborate in the light of the fact that only "current practice" is being described. However, although there is a general idea of "current practice", exact protocols do differ from laboratory to laboratory. Therefore, it is important to specify exact protocols followed. Only this way, thorough comparison and evaluation of success is possible.

Guatteria

Total genomic DNA was extracted using a modified cetyl trimethyl ammonium bromide (CTAB) method (Doyle & Doyle, 1987), a method that performs comparatively well for the extraction of DNA from herbarium specimens (Drábková & al., 2002). 0.05 g Leaf material was weighed for each sample (large veins were removed); this material was put into a to 65°C preheated pestle with some fine sand and ground to rough powder with a mortar; 650 µl CTAB solution was added and ground further; another 650 µl CTAB solution was added, mixed, and the whole content of the pestle poured into a 2 µl eppendorf tube; 12 µl β-mercaptoethanol was pipetted into the eppendorf tube and mixed again; the eppendorf

Table 1. Information on the extractions from the Rauwolf Herbarium at Leiden Herbarium (L). The German physician Leonhard Rauwolf collected these plants on a trip to the Middle East in the years 1573-75. Ng/ µl DNA extracted, DNA extraction success (0=no result; 1=successful extraction) and amplification success (0=no result; 1=successful amplification). An @ behind the page number indicates specimens that were extracted with a modified CTAB method. Identifications of specimens were done using a combination of Blast search result from GenBank (number of equal hits from search are in parentheses next to percentage match), visual identification of specimen, and record of plants collected by Rauwolf (Dannenfeldt, 1968). An asterisk next to the genus name indicates that this was recorded as collected by Rauwolf.

Rauwolf page number	**Family**	**Genus**	**Blast percentage on best hit (# of hits with top score)**	**Success in extraction**	**ng/ µl DNA extracted**	**Successfull amplification**
19	Poaceae	several	97 (17)	1	4.3	1
34	Fabaceae	Pisum	95 (1)	1	1.5	1
30	Fabaceae	Astragalus*	95 (1)	1	12.0	1
30@	Fabaceae	Astragalus*	95 (1)	1	55.8	1
41	Hemerocallidaceae	Hemerocallis*	98 (1)	1	38.2	1
64	Solanaceae	Solanum*	98 (11)	1	2.4	1
64@	Solanaceae	Solanum*	98 (11)	1	20.5	1
203	Asteraceae	Carthamus*	98 (17)	1	7.2	1

tube was transfered into a 65°C water-bath and left there for 15-20 minutes, mixing thoroughly at least every 5 minutes; thereafter the eppendorf tube was topped off with a 24:1 chloroform:isoamylalcohol mixture almost to the rim and placed in a rocking machine for at least 1½ hours; finally, the tubes were centrifuged at 14,400 rpm for 10 minutes and the top phase was pipetted into a new eppendorf tube.

Purification was done using the Wizard PCR Preps DNA Purification System (Promega Corp.) or the Wizard DNA Clean-up System (Promega Corp.) in combination with a vacuum manifold (Vac-Man Laboratory Vacufold, Promega Corp.) with syringes. The DNA was dissolved in 30 µl pre-heated elution buffer (Qiaquick PCR Purification Kit, Qiagen). Extraction was considered successful when a band of total DNA or a DNA smear was visible on a 0.6-1.0% agarose gel and unsuccessful if not.

<u>*Zehneria*</u>

The *Zehneria* specimens were extracted using the DNeasy plant DNA extraction kit (Qiagen) with modifications. All herbarium material was extracted in a separate facility, using dedicated equipment and reagents. For each sample, about one cm^2 of leaf material was removed from the herbarium sheet with a sterile forceps and placed in a 1.5 ml tube. Sterile 3 mm glass beads and sea sand were placed in the tubes and the leaf material was then ground inside the tube using a Retsch Mill (Retsch Co.). The rest of the extraction proceeded according to the instructions provided by Qiagen, modified for museum material by extending incubation times, the addition of proteinase k (10-20 µl), and additional wash with 100% Ethanol (if necessary). After extraction buffer was added, samples were generally incubated from six hours to overnight. After incubation and spinning sample through the Qiashredder column (Qiagen), additional binding buffer was added and this mixture was kept on ice for 20 minutes. For the final elution, 50-75 µl (about half of the prescribed amount) of Buffer AE (or alternatively $TE_{0.1}$) was added, and then incubated for up to an hour at room temperature, before spinning into a fresh 1.5 ml tube. The quantity of DNA for these extractions was measured using a Nanodrop spectrophotometer (Nanodrop Technologies). A working aliquot of each extraction was made, and the bulk was stored in the freezer.

Rauwolf herbarium

The Rauwolf specimens were extracted using both a modified CTAB extraction procedure (Doyle & Doyle, 1987), as well as with the DNeasy extraction kit (with modifications as described under *Zehneria*). Because of their age, the Rauwolf specimens were extracted at the Leiden Ancient DNA Facility. The quantity of DNA for these extractions was measured using a Nanodrop spectrophotometer (Nanodrop Technologies).

DNA amplification

Guatteria

To test if the extracted DNA was suitable for amplification two plastid markers were used. The primers 1F/724R (Olmstead & al., 1992) were used to partially amplify the *rbcL* gene (c. 700 bp). To check if specimens that did not amplify with this primer combination could be amplified in smaller fragments primers 217F and 536R (Pirie & al., 2005b) were used. The *trnL* intron (c. 600 bp) was amplified using the standard c and d primers (Taberlet & al., 1991). Because these regions are rather large, they can be seen as a measure of the quality of the DNA extracted in terms of its degradation. A standard reaction mix (2.5 µl 10x Taq Buffer without $MgCl_2$ (Sigma-Aldrich); 3.5 µl $MgCl_2$ (25 mM; Sigma-Aldrich); 1.0 µl DNTP's (5 µM each); 0.25 µl forward primer (25 µM); 0.25 µl reverse primer (25 µM); 0.5 µl 'Red' Taq polymerase (Sigma-Aldridge, 1 U/µl); 1.0 µl BSA (0.4%); 15.5 µl H_2O; 0.5 µl DNA; total volume 25.0 µl), PCR protocol (35 cycles; 30 sec.: 94°C; 30 sec.: 53°C; 1 min.: 72°C; with an initial 5 min.: 94°C and final 10 min.: 72°C) and ABI 9700 Thermal Cycler (Applied Biosystems) were used. Amplicons were purified using a Qiaquick PCR Purification Kit (Qiagen). Amplification was scored as failed when no regions could be amplified, partially successful if only one region gave a visible band on a 1.5% agarose gel and as working when both regions were successfully amplified.

Zehneria

For the *Zehneria* study, two plastid markers and a single-copy nuclear gene were amplified (specifications available from H. Cross, unpublished). The plastid markers *trnL-F* spacer and *trnK* spacer produced PCR products of c. 440 bp and c. 180 bp, respectively. A portion of the nuclear gene *Glyceraldehyde Phosphate Dehydrogenase* (GAP), corresponding to exons 7-9 of the *Arabidopsis* sequence, was amplified using several internal primers with products ranging in size from 200-750 bp. For the Rauwolf specimens, a 120 bp portion of the plastid *rbcL* gene was amplified using the primers Z1af and 19br (Hofreiter & al., 2000). The PCR reactions contained 2.5 µl of 10x Taq buffer with 15 mM $MgCl_2$, 1 µl dNTPs (10 uM), 1.25 µl BSA (1 mg/ml), 0.25 µl Qiagen Taq polymerase, and 17 µl H_2O. The thermal cycler (MJ Research PTC 100) reactions for these reactions were: initial denaturation of 94°C for three minutes, followed by 35 cycles of 94°C for 25 sec., 54°C for 60 sec., and 72°C for 45 sec., followed by an extended elongation phase of 5 min. at 72°C. All PCR products were purified using Qiagen PCR purification kit (Qiagen).

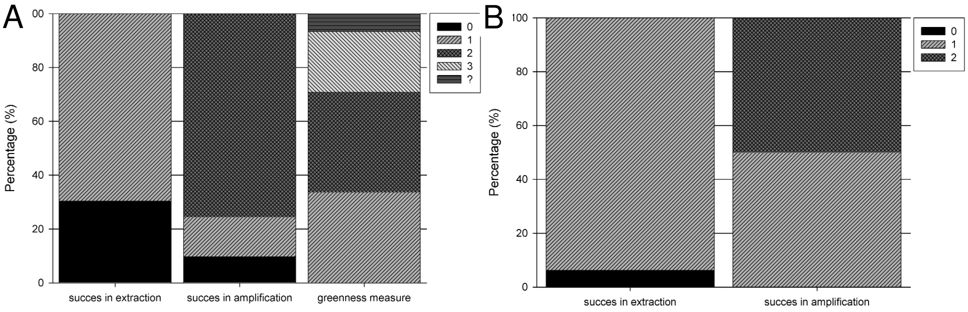

Figure 2. DNA extraction success (0=no result; 1=successful extraction) and amplification success (0=no result; 1=partial result (*trnL* intron or *rbcL*) 2=both markers amplified; (un)successful amplification was calculated as a percentage of the specimens that had a successful extraction) and greenness of leaf tissue measure (1=brown; 2=green/brown; 3=green) for A. *Guatteria* study and B. *Zehneria* study. Leaf greenness data was not available for *Zehneria* specimens. Complete voucher information and base data in tables 3 & 4.

Rauwolf herbarium

For the Rauwolf specimens, a 120 bp portion of the plastid *rbcL* gene was amplified using the primers Z1af and 19br (Hofreiter & al., 2000). PCR reaction mix, thermal cycling specifications and PCR product purification as described under *Zehneria.*

Statistical analysis

Statistical analyses were performed using the SPSS 13.0 for Windows, software package (SPSS Inc. 1989-2004). To test if age and greenness of the leaves are linked to DNA extraction and amplification success a logistic regression analysis was applied with the Backward stepwise (Likelihood Ratio) method. For the single analyses the *P*-values from the "model if term removed"-box are reported and for the combined analyses the omnibus coefficients are presented (omnibus statistics are tests that can reflect the combined significance of several independent tests of a common hypothesis).

RESULTS

DNA extraction success

105 out of 151 *Guatteria* specimens yielded a positive extraction result (69%; figure 2A). The oldest specimens of which DNA was extracted and successfully amplified were *Guatteria sordida* var. *ovalis* and *G. sordida* var. *lanceolata,* both 168 years old, the youngest specimens were seven years old (*G. schlechtendaliana* and *G. pogonopus*). No DNA could be extracted from the youngest (six years old) or the oldest (184 years old) herbarium specimen. For the *Zehneria* study, DNA could be extracted from 60 out of 64 specimens (94%; figure 2B). The oldest specimen for which DNA was obtained from this study was *Cucumis melo*, which was 188 years old. A specimen of *Diplocyclos palmatus*, was the oldest cucurbit at 240 years, but did not yield any DNA. The specimens from the Rauwolf herbarium were by far the oldest reported in this study, and all eight specimens from this c. 430 year-old collection produced low amounts of DNA that could be used to amplify the target region (table 1).

Guatteria data

There is no relationship between the age and the greenness of the leaves (p=0.675; table 2), i.e. old leaves do not tend to be browner. Furthermore, the trichotomy in greenness (green,

green/brown or brown) did not prove to have any extra explanatory power in the tests described below. Therefore, all analyses were performed with the dichotomous measure green versus non-green (green/brown and brown together).

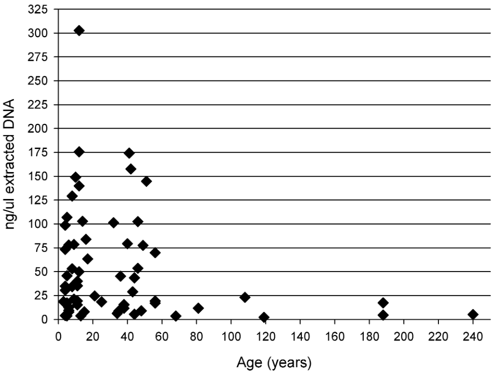

Figure 3. Amount of DNA (ng/µl) extracted as a function of the age of the specimens for the *Zehneria* study.

The relationship between the extraction success of a specimen and the age or the greenness of the leaf tissue is non-significant (p=0.084 and p=0.073 respectively; table 2). If age and greenness are taken together in the analysis as covariants there is a significant relationship (p=0.044). This means that DNA is easier extracted from young green leaves than from old brown leaves. On the other hand, DNA from young brown leaves might be as easy or difficult to extract as from old green leaves.

When amplification success (dichotomized as "not/partially working" versus "both regions amplified" or as "not working" versus "one/both regions amplified") is tested for a relationship with age and greenness, age (p=0.007 and p=0.008 respectively; table 2) and greenness (p=0.004 and p=0.020 respectively; table 2) both show a significant relationship. Age and greenness analyzed together show an even stronger relationship (p=0.002 and p<0.001 respectively; table 2). This indicates that it is easier to obtain an amplicon from young leaves and green leaves than from old or brown leaves. Next to this, young green leaves are preferable over old brown leaves in order to obtain an amplicon.

If DNA is successfully extracted from a specimen, amplifications are likely to work (chi-square test; p<0.001). Of the 105 successfully extracted specimens of *Guatteria* 78 (76%) amplified for both markers, 15 (14.5%) amplified only for one of the two markers used and only 10 (9.5%) specimens did not amplify at all (figure 2A).

Zehneria and Rauwolf data

There is no linear relationship between the age of the samples and the quantity of DNA extracted (figure 3). However, the relationship between the age of the samples and the log of the quantity of DNA extracted is highly significant (p=0.009; table 2). For each year a specimen ages, the amount of DNA extracted decreases c. 1%. The data also show a relationship between age and amplification success, when scored as successful versus

Table 2. Summary table for obtained *p*-values for different statistical tests with regard to the age, greenness of leaves and extraction and amplification success, using multiple regression analyses. n.s. = not significant.

Relation between:	age	extraction success	extraction success	extraction success	amplification success	amplification success	amplification success
and:	greenness	age	greenness	age and greenness	age	greenness	age and greenness
Guatteria	n.s.	n.s.	n.s.	$p < 0.05$	$p < 0.01$	$p < 0.01$	$p < 0.01$
Zehneria	---	$p < 0.01$	---	---	$p < 0.05$	---	---

(partially) successful amplification of three gene regions ($p=0.024$; table 2). This indicates that for the included Cucurbitaceae specimens age can be used as a marker when selecting specimens for DNA extraction.

Amplifications always (partially) worked when DNA was successfully extracted from a specimen (chi-square test; $p<0.001$). Of the 60 successfully extracted specimens 30 (50%) amplified for all three markers and 30 (50%) amplified for two markers used (figure 2B). The small fragment of *rbcL* was successfully amplified from all of the Rauwolf specimens (table 1).

DISCUSSION

Age and the greenness of leaves are thought to be axiomatic indicators for DNA extraction and amplification success when selecting herbarium specimens for molecular studies. These indicators are easily determined and they could be important for DNA isolation DNA for several reasons. Age is an important factor because DNA degrades with time (Foran, 2006) and specimens in a herbarium are not stored for optimal DNA conservation but for optimal conservation of the visual appearance of the specimen (Bridson & Forman, 1992). The greenness of the leaf tissue can be used as an indicator for the presence of plastids and these are often targeted for the amplification of DNA in phylogenetic studies. However, the link between these two factors and DNA extraction success is not always clear. So far, only some small scale studies have shown that there might be no actual relationship between age and extraction success (e.g. Drábková & al., 2002; Jankowiak & al., 2005).

Given the long period of time that DNA extraction and amplification have been undertaken, statistical tests for DNA extraction and amplification success might be seen as superfluous. It could also be argued that these tests should be carried out in an experiment designed to include a greater diversity of samples from a wider age range than presented here. However, such experiments will likely never be done. Few laboratories have sufficient budgets and material to make available for such a large-scale, controlled study. In addition, not one but many labs working on different plant groups should engage in such an effort in order to compare results between different taxa. Therefore, as the beginning of a discussion on herbarium specimen use in molecular research, data from three different studies on different plant groups were compared here. Furthermore, already much data is available from many plant studies that have not been reported. It is hoped that more comparative studies as this one will be published.

As shown here, for 151 *Guatteria* herbarium specimens there is no relationship between age and the extraction success of DNA (table 2) and at first sight this corroborates the earlier qualitative findings of Rogers & Bendich (1985), Savolainen & al. (1995), Drábková & al. (2002) and Jankowiak & al. (2005). These small scale studies reported that DNA was successfully extracted from an old specimen and the authors therefore suggested that an apparent correlation between age and DNA extraction or amplification success did not exist. The large *Guatteria* data set seems quantitatively to show that this correlation indeed does not exist.

However, there might be a methodological pitfall here. Quantification of DNA on gel, as was done in the *Guatteria* study, might not be specific enough to score extraction success and therefore age might erroneously fail to show a relationship with successful extractions. This idea is supported by the fact that a relationship between age and extraction success does exist in the *Zehneria* data, where the amount of extracted DNA decreased with c. 1% per year. This would mean that the suggested absence of a relationship between age and extraction success in the above mentioned studies is not general.

Next to age, greenness is often used as a visual cue for selecting suitable specimens. Here it is shown that the greenness of the leaves does not predict the extraction success of a specimen well (table 2). Furthermore, the age of the specimen is not related to the greenness of the leaves, i.e. older specimens do not tend to be browner (table 2). This fact seems to support the relationship between the colour of the leaf and the method of drying (suggested by Jankowiak & al., 2005) and perhaps the way the specimen was subsequently stored (Bridson & Forman, 1992), both factors determining the quality of the conservation of the DNA. Alternatively, some plant leaves of specific taxa always turn brown upon drying, regardless of the drying method (e.g. de Wilde & Duyfjes, 2006).

The method of drying is a crucial factor in order to obtain amplifiable DNA because of the metabolic and cellular processes that damage the DNA when the plant is not dried rapidly enough (Savolainen & al., 1995). Rapid drying is often done with the use of open fire (e.g. burners), and is mostly accompanied by high temperatures (sometimes even burning the specimens). However, the influence of high temperatures on DNA is not straightforward. A study on DNA extraction from charred seeds (Threadgold & Brown, 2003) showed that seeds that were heated to 150°C or 200°C up to 5 hours still yielded amplifiable DNA, while seeds heated up to 225°C or 250°C for a short period of time gave no results. To determine in retrospect how hot specimens were when dried is of course impossible. However, it has been shown that using a low temperature air-flow method to dry specimens, can help to retain the natural colours of the specimens. Furthermore, these specimens are often more suitable for extraction of DNA (Blanco & al., 2006). Such drying method is therefore preferable if no leaves are specifically dried on silica gel.

Next to drying temperature, there are numerous biological features of plants that can influence extraction and amplification results (Rogers & Bendich, 1985; Savolainen & al., 1995). However, the extraction method and the PCR program and primers used are also crucial in order to obtain good results. The influence of the extraction method is clear from the Rauwolf study in which two specimens were extracted with two different extraction methods (table 1) and the modified CTAB method yielded much more DNA. In the *Guatteria* study a similar phenomenon was observed (data not shown). In general the CTAB method yields more DNA than silica-column-based kits (data not shown), largely because not all DNA will bind to the silica when passing through the column, and much can be lost. However, because silica binds very specifically to DNA, extractions with this method can often result in cleaner DNA. It is recommended for older material to extract with a CTAB method, to obtain as much DNA as possible, and if further cleaning is necessary, to take an aliquot of the extractant and purify this through a silica column. Additionally, for more degraded material, further cleaning with silica columns designed for PCR purification, which are designed to bind to smaller fragments of DNA (e.g. Qiagen Qiaquick columns) may yield more DNA. This has been found in other ancient DNA studies as well (Yang & al., 1998). Furthermore, the *Guatteria* study reported here also successfully applied this modification (see methods section).

With regard to optimizing amplification success, the use of a Nanodrop might be worthwhile. Where initial amplifications fail it is important to find out what the nature of the extracted DNA is: low amounts of good quality DNA or large amounts of degraded DNA. Different approaches are recommended to address these two problems. For the first case: low amounts of generally good quality DNA, several studies have reported success using nested PCR (Grote & al., 2002; Zeng & al., 2005). In this procedure, external primers are used in an initial round of PCR and the products of this reaction are then used as the template for a second round of PCR in which internal primers are used. This has been used successfully from as low as a few *femto*grams of DNA (Zeng & al., 2005).
For the second case, where there is more DNA but it is heavily degraded (and which is more often the case for herbarium specimens), two easily applicable, though often overlooked, improvements for enhancing amplification success can then be applied: the use of internal primers (to amplify a smaller fragment) and/or more specific primers. Both improvements work for good quality DNA but especially for degraded DNA internal primers are a requisite. Seven *Guatteria* accessions that did not amplify for the *rbcL* region (using standard primers 1F-724R), could be amplified using internal primers for that region (specimens indicated in table 3), thus reducing length of the fragment from c. 700 bp to only c. 400 bp. The same result was found in the *Zehneria* study, in which a single nuclear gene of c. 700 bp could not be amplified in several older specimens as one amplicon, but using several PCRs with overlapping internal primers of 200-300 bp were successful (H. Cross, unpublished). Furthermore, designing specific primers for the group under study, instead of using the general primers, can also aid the chances of obtaining the target amplicon and lessen the risk of contamination. Because the target DNA is present in much smaller quantities than with freshly extracted material, any background contamination co-extracted with the sample will have a much more negative effect on the efficacy of the PCR.

The combination of age and greenness of the leaves (or age by itself in the case of *Zehneria*) can be used to estimate success in extraction and amplification (table 2). DNA in young green leaves is extracted more easily than DNA in old brown leaves, a non-surprising conclusion. Therefore, researchers will always maximize the chance of success by using fresh, young leaf material if possible. However, the interesting specimens are the young-brown leaves, old-green leaves and greenish brown leaves (of any age). In cases where for instance only old-green material is available, most researches will still attempt to obtain results simply because this material represents their only source. This study shows that in the case of rare old specimens, researchers should perhaps refrain from using these specimens (or use a non-destructive method, Rohland & al., 2004) because chances of success are unpredictable and precious herbarium material might be wasted if unsuccessful. The uncritical use of axiomatic indicators such as age or leaf colour is therefore not recommended.

It appears from this and previous studies that one of the most important factors for successful DNA extraction from a plant is what happens to the specimen between the time it is collected to when it is safely stored on an herbarium shelf. In many remote localities there is no drying oven at hand and sometimes there is a significant lapse of time until the specimen can be properly dried. This is especially difficult in humid areas, such as tropical rainforests that ironically contain the highest plant diversity. Even after drying the specimen is often stored and shipped in moist conditions. To combat this problem, field researchers have often soaked or sprayed their plant collections with alcohol, and while this helps keep the specimens from getting mouldy and decaying, the water in the alcohol can continue to degrade the DNA. Herbarium collections that have been collected in alcohol are usually very difficult to use for molecular work. The overriding problem is that this knowledge, like so much else, is not generally known to the person attempting to use the specimen for extraction. Much of what happens to the plant on its way to the herbarium is not recorded and can only be guessed at from the field notes and general information about the locality and standard practice. Therefore, if leaf material is not specially silica-dried for molecular studies, botanists should annotate how the herbarium specimens were collected and dried and preferably put this information on the label.

Because successful extractions are so often specific to a particular family or even genus of plants, the above mentioned factors may work well as guidelines within certain groups, and not at all in others. Therefore, more data on success of DNA amplification and extraction is needed to be able to formulate more general rules. As is shown here, age itself is not a strong predictor for success in *Guatteria*, however, for *Zehneria* extractions from older specimens do tend to yield lower amounts of DNA. This result contradicts the previously suggested absence of such a relationships (Rogers & Bendich, 1985; Savolainen & al., 1995; Drábková & al., 2002; Jankowiak & al., 2005). On the contrary, the ongoing Rauwolf study shows that even exceptionally old specimens can still yield DNA. It can be recommended that researchers should report the success rate when using herbarium specimens and what specific extraction method, PCR protocol etc. has worked for particular groups. Herbarium material is a precious commodity, and is often the only remaining floral record of now extinct ecosystems. It would be a tremendous waste of this material and time for researchers to continually repeat the same errors.

Even after 20 years of herbarium specimen use for DNA extraction, it is still difficult to draw up general recommendations for criteria to evaluate these specimens in relation to the likelihood of successful DNA extraction and amplification. Nevertheless, it is clear that axiomatic indicators such as the age or greenness of the leaf tissue do not always provide good estimates of success, but do at least provide a starting point for evaluation. General knowledge of the group under study, sound lab practice and experience, as well as gut feeling at this point might still provide the best chance of success. Hopefully, the results presented here can be the starting point for a more thorough search for useful criteria.

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Table 3. *Guatteria* voucher information, age, DNA extraction success (0=no result; 1=successful extraction) and amplification success (0=no result; 1=partial result (*trnL* intron or *rbcL*) 2=both markers amplified) and greenness of leaf tissue measure (1=brown; 2=green/brown; 3=green; ?=unknown). An @ in the amplification success column indicates specimens on which internal *rbcL*-primers have been tried. Type specimens of species that have been synonymized are listed under their basionym, with the accepted species name in between brackets.

UDNA nr.	Genus	Species	Collector	Collection Number	Herbarium	Collection date	Age (absolute)	Success in extraction	Successfull amplification	Greenness measure
794	*Guatteria*	*glabrescens*	Maas, P.J.M.	8816	U	05/01/1999	6	0	0	2
807	*Guatteria*	*pogonopus*	Kollmann, L.	202	U	09/07/1998	7	1	2	3
802	*Guatteria*	*schlechtendaliana*	Kollmann, L.	871	U	29/10/1998	7	1	2	1
822	*Guatteria*	*multivenia*	Maas, P.J.M.	8611	U	05/02/1997	8	1	2	3
830	*Guatteria*	*guentheri*	Acevedo-Rdgz., P.	8973	U	22/01/1997	8	0	0	1
779	*Guatteria*	*dumetorum*	FLORPAN	2497	U	14/03/1996	9	1	2	2
1393	*Heteropetalum*	*brasiliense*	Acevedo-Rdgz., P.	8266	K	13/08/1996	9	1	1	1
941	*Heteropetalum*	*brasiliense*	Acevedo-Rdgz, P.	8076	U	08/08/1996	9	0	0	1
816	*Guatteria*	*stipitata*	Jaramillo, N.	820	U	09/10/1995	10	1	2	2
1396	*Guatteriopsis*	*hispida*	Miralha, J.M.S.	295	K	01/10/1995	10	1	2	?
834	*Guatteria*	*decurrens*	Maas, P.J.M.	8314	U	09/11/1994	11	1	1 @	2
823	*Guatteria*	*modesta*	Dulmen, A. van	183	U	07/11/1993	12	1	2	3
790	*Guatteria*	*macropus*	Pirani, J.R.	2725	U	30/01/1993	12	1	2	1
797	*Guatteria*	*citriodora*	Ribeiro, J.E.L.S.	964	U	01/07/1993	12	1	1	1
950	*Guatteriopsis*	*hispida*	Ribeiro, J.E.L.S.	845	U	04/06/1993	12	1	1	1
786	*Guatteria*	*caribaea*	Tuxill, J.	89	U	01/05/1992	13	1	2	3
1391	*Guatteriopsis*	*friesiana*	Dick, C.W.	79	K	26/03/1992	13	1	2	2
1390	*Guatteriopsis*	*friesiana*	Dick, C.W.	5	K	25/02/1992	13	1	1	2
800	*Guatteria*	*cuatrecasassii*	Gudiño, E.	1272	U	06/02/1991	14	0	0	2
1394	*Heteropetalum*	*brasiliense*	Berry, P.E.	5044	K	03/07/1991	14	1	1	1
840	*Guatteria*	*amazonica*	Grández, C.	2915	U	24/10/1991	14	0	0	1
795	*Guatteria*	*dusenii*	Hatschbach, G.	53736	U	24/01/1990	15	0	0	3
949	*Guatteriopsis*	*friesiana*	Lepsch Cunha, N.M.	932	U	07/02/1990	15	0	0	2
837	*Guatteria*	*calophylla*	Vásquez, R.	14341	U	08/09/1990	15	0	0	1
945	*Guatteriella*	*tomentosa*	Murillo, J.	538	U	09/07/1989	16	1	0	2
944	*Guatteriella*	*tomentosa*	Cid F., C.A.	9987	U	18/01/1989	16	1	0	1
947	*Guatteriopsis*	*blepharophylla*	Cuello, N.	619	U	28/01/1989	16	0	0	1
817	*Guatteria*	*sphaerantha*	Faber-Langendoen, D.	1556	U	29/06/1988	17	1	2	3
819	*Guatteria*	*pittieri*	Werff, H.H. van der	9767	U	26/01/1988	17	1	2	3
813	*Guatteria*	*nigrescens*	de Lima, H.C.	3405	U	18/07/1988	17	0	0	3
820	*Guatteria*	*peruviana*	Murillo, J.	643	U	12/07/1998	17	0	0	3
784	*Guatteria*	*sessilicarpa*	McPherson, G.	12599	U	19/06/1988	17	1	2	2
821	*Guatteria*	*pacifica*	Gentry, A.H.	62881	U	13/06/1988	17	1	2	2
814	*Guatteria*	*venezuelana*	Wingfield, R.	6688	U	30/08/1978	17	1	2	1
942	*Heteropetalum*	*spruceanum*	Stevenson, D.W.	1115	U	04/12/1987	18	1	2	3
811	*Guatteria*	*oligocarpa*	Maas, P.J.M.	7006	U	25/11/1987	18	1	2	2
833	*Guatteria*	*elegantissima*	Gentry, A.H.	56948	U	16/04/1987	18	1	2	2
825	*Guatteria*	*longicuspis*	Stergios, B.	9763	U	16/01/1987	18	0	0	2

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781	*Guatteria*	*jefensis*	Valdespino, I.A.	685	U	22/04/1987	18	1	2	1
948	*Guatteriopsis*	*blepharophylla*	Hahn, W.	3656	U	28/07/1987	18	1	2	1
1392	*Heteropetalum*	*spruceanum*	Kawasaki, M.L.	235	K	22/11/1987	18	1	2	1
832	*Guatteria*	*excellens*	Díaz, P.	85	U	02/10/1986	19	1	2	3
1405	*Guatteriella*	*tomentosa*	Daly, D.C.	4494	U	09/12/1986	19	1	2	2
1388	*Guatteriella*	*tomentosa*	Daly, D.C.	4494	K	09/12/1986	19	1	1	2
792	*Guatteria*	*liesneri*	Cid F., C.A.	8403	U	04/10/1986	19	1	2	1
829	*Guatteria*	*heterotricha*	Monsalve B., M.	1262	U	13/11/1986	19	1	2	1
824	*Guatteria*	*macrocarpa*	Berg, C.C.	1560	U	11/07/1986	19	1	1	1
838	*Guatteria*	*boliviana*	Solomon, J.C.	10789	U	12/09/1985	20	1	2	3
785	*Guatteria*	*blainii*	Maas, P.J.M.	6443	U	28/03/1985	20	1	2	2
828	*Guatteria*	*insculpta*	Boom, B.M.	5586	U	04/02/1985	20	0	0	2
815	*Guatteria*	*trichoclonia*	Schunke V., J.	14061	U	16/07/1984	21	1	2	3
782	*Guatteria*	cf *lucens*	GƦmez, L.D.	23305	U	07/11/1984	21	1	2	2
826	*Guatteria*	*liesneri*	Kral, R.	71950	U	03/12/1984	21	1	2	2
841	*Guatteria*	*alta*	Gentry, A.H.	48250	U	17/07/1984	21	1	2	2
835	*Guatteria*	*crassipes*	Juncosa, A.	1962	U	27/01/1984	21	0	0	2
943	*Heteropetalum*	*spruceanum*	Stergios, B.	7685	U	05/12/1984	21	0	0	1
780	*Guatteria*	*inuncta*	Liesner, R.L.	14631	U	21/04/1983	22	1	2	1
803	*Guatteria*	*rupestris*	CFCR	4116	U	28/02/1983	22	1	2	1
791	*Guatteria*	*longicuspis*	Maas, P.J.M.	6835	U	22/10/1987	22	0	0	1
827	*Guatteria*	*latisepala*	Sánchez, D.	404	U	10/10/1982	23	1	2	3
799	*Guatteria*	*burchellii*	de Carvalho, A.M.	661	U	29/04/1981	24	1	2	2
818	*Guatteria*	*sessilis*	Liesner, R.	8546	U	21/01/1980	25	1	2	2
796	*Guatteria*	*curvinervia*	Gottsberger, G.	11-15168	U	15/01/1968	27	1	2	2
805	*Guatteria*	*pubens*	Spada, J.	198	U	16/05/1978	27	1	2	2
787	*Guatteria*	*neglecta*	Gottsberger, G.	11-12268A	U	12/11/1968	27	1	2	1
789	*Guatteria*	*mexiae*	Mori, S.A.	9722	U	19/03/1978	27	1	2	1
1389	*Guatteriopsis*	*blepharophylla*	Prance, G.T.	P25063	K	20/12/1977	28	1	2	2
783	*Guatteria*	*rotundata*	Mori, S.A.	5531	U	12/04/1975	30	1	2	2
776	*Guatteria*	*alata*	Mori, S.A.	2894	U	31/10/1974	31	1	2	3
777	*Guatteria*	*allenii*	Mori, S.A.	2952	U	02/11/1974	31	1	2	3
793	*Guatteria*	cf *hilariana*	Gottsberger, G.	21-9274A	U	09/11/1974	31	1	2	3
798	*Guatteria*	cf *candolleana*	Harley, R.M.	17360	U	24/03/1974	31	1	2	2
951	*Guatteriopsis*	*ramiflora*	Schunke V., J.	8073	U	05/08/1974	31	1	2	1
1404	*Guatteria*	*galeottiana*	Beaman, J.H.	6121	U	10/07/1972	33	1	2	3
806	*Guatteria*	*pohliana*	Anderson, W.R.	35703	U	09/02/1972	33	1	2	1
801	*Guatteria*	*brevicuspis*	Prance, G.T.	16328	U	23/11/1971	34	1	2	3
812	*Guatteria*	*notabilis*	Irwin, H.S.	27980	U	20/03/1970	35	1	2	3
870	*Guatteria*	*schunkevigoi*	Schunke V., J.	3551	S	23/10/1969	36	1	2	2
831	*Guatteria*	*flexilis*	Marcano-Berti, L.	755	U	29/05/1969	36	0	0	2
940	*Heteropetalum*	*brasiliense*	Farinas, M.	645	U	01/01/1969	36	0	0	1
809	*Guatteria*	*parvifolia*	Gottsberger, G.K.	573007	U	03/04/1968	37	1	2	3
946	*Guatteriella*	*campinensis*	Prance, G.T.	3814	U	21/12/1966	39	1	0	1
808	*Guatteria*	*poeppigiana*	Prance, G.T.	1775	U	29/10/1965	40	1	2	3
804	*Guatteria*	*rigida*	Irwin, H.S.	6670	U	04/10/1964	41	1	2	2
836	*Guatteria*	*cardoniana*	Breteler, F.J.	3932	U	07/05/1964	41	0	0	2
876	*Guatteria*	*stenopetala*	Maguire, B.	42558	S	31/12/1957	48	1	0	1
927	*Guatteria*	*bernardii* (*G. schomburgkiana* Mart.)	Bernardi, A.L.	6534	S	14/04/1957	48	0	0	?
1395	*Guatteria*	*riparia*	Maguire, B.	34835	K	04/04/1953	52	1	2	2
901	*Guatteria*	*maguirei*	Maguire, B.	35231	S	12/02/1953	52	0	0	2
892	*Guatteria*	*procera*	FDBG	3676	S	26/11/1942	53	0	0	1
918	*Guatteria*	*denundata*	Schultes, R.E.	17374	S	10/09/1952	53	0	0	1
880	*Guatteria*	*velezii* (*G. maypurensis* Kunth)	Velez, I.	2488	S	23/04/1946	59	1	2	1
931	*Guatteria*	*lehmannii*	Cuatrecasas, J.	22297	S	22/10/1946	59	1	2	?
887	*Guatteria*	*pacifica*	Cuatrecasas, J.	17150	S	30/04/1944	61	1	2	2

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875	*Guatteria*	*sphaerantha*	Cuatrecasas, J.	17579	S	15/05/1944	61	0	0	2
920	*Guatteria*	*chocoensis*	Cuatrecasas, J.	16592	S	10/03/1944	61	1	?	1
923	*Guatteria*	*calimensis*	Cuatrecasas, J.	16566	S	10/03/1944	61	0	0	1
881	*Guatteria*	*venezuelana*	Steyermark, J.A.	55097	S	30/12/1943	62	1	2	2
882	*Guatteria*	*verruculosa*	Fosberg, F.R.	19126	S	16/12/1942	63	1	2	3
926	*Guatteria*	*brachypoda*	FDBG	3474	S	23/06/1942	63	1	1 @	2
883	*Guatteria*	*williamsii*	Williams, L.	15559	S	26/05/1942	63	1	1	1
912	*Guatteria*	*glaberrima*	Lugo, M.	237	S	25/04/1940	65	0	0	?
910	*Guatteria*	*gracilipes*	Krukoff, B.A.	1156	S	01/09/1939	66	1	2	3
839	*Guatteria*	cf *lasiocalyx*	Krukoff, B.A.	11086	U	08/10/1938	67	1	2	2
902	*Guatteria*	*metensis*	Haught, O.	2470	S	19/12/1938	67	1	0 @	2
896	*Guatteria*	*rigidipes*	Skutch, A.F.	2553	S	01/02/1936	69	1	2	3
873	*Guatteria*	*speciosa*	Ducke, A.	29049	S	16/11/1936	69	1	2	1
897	*Guatteria*	*kuhlmanii*	Kuhlman, J.G.	RB24256	S	17/09/1936	69	0	0	1
914	*Guatteria*	*ecuadorensis*	Mexia, Y.	711	S	28/03/1935	70	1	2	?
925	*Guatteria*	*brevipedicellata*	Lawrence, G.E.	771	S	27/04/1933	72	1	2	2
899	*Guatteria*	*lawrencei*	Lawrence, G.E.	215	S	14/06/1932	73	0	0	3
810	*Guatteria*	*paraensis*	Froes, R.	1753	U	06/07/1932	73	1	2	1
889	*Guatteria*	*parvifolia*	Hoehne, F.C.	SP28405	S	28/10/1931	74	1	0 @	3
929	*Guatteria*	*allenii*	Allen, P.H.	1900	S	09/07/1939	74	0	0	3
916	*Guatteria*	*duckeana*	Ducke, A.	RB29019	S	01/06/1935	74	1	?	?
788	*Guatteria*	*minarum*	Mexia, Y.	5131	U	01/10/1930	75	0	0	2
869	*Guatteria*	*sabuletorum*	Ducke, A.	RB19617	S	25/01/1927	78	1	2	1
877	*Guatteria*	*trichoclonia*	Buchtien, O.	698	S	01/11/1926	79	1	2	3
878	*Guatteria*	*umbonata*	Ducke, A.	19614	S	25/03/1926	79	1	0 @	2
900	*Guatteria*	*longistipitata*	Ducke, A.	RB23699	S	16/06/2026	79	0	0	2
924	*Guatteria*	*buchtienii*	Buchtien, O.	699	S	01/12/1926	79	0	0	1
888	*Guatteria*	*parviflora*	Kuhlman, J.G.	RB24263	S	18/03/1924	81	1	0 @	2
884	*Guatteria*	*obliqua*	Kuhlman, J.G.	RB24280	S	17/10/1923	82	1	1	1
911	*Guatteria*	*glabrescens*	Kuhlman, J.G.	RB4483	S	11/01/2022	83	0	0	?
919	*Guatteria*	*curvinervia*	Frazao, A.	8667	S	01/07/1917	88	0	0	2
885	*Guatteria*	*odorata*	Ducke, A.	MG15722	S	16/03/1915	90	1	1	1
928	*Guatteria*	*augusti*	Weberbauer, A.	7062	S	07/08/2014	91	0	0	1
907	*Guatteria*	*jamundensis*	Ducke, A.	MG11780	S	18/05/1911	94	0	0	2
915	*Guatteria*	*dusenii*	Dusén, P.	13752	S	21/12/1911	94	1	2	?
913	*Guatteria*	*fruticosa*	Lofgron, A.	4059	S	14/12/2009	96	0	0	3
891	*Guatteria*	*polycarpa*	Dusén, P.	7414	S	30/12/1908	97	1	2	3
906	*Guatteria*	*neglecta*	Dusén, P.	6780	S	30/09/2008	97	1	1	3
890	*Guatteria*	*polyantha*	Costa, R.C Monteiro da	284	S	15/04/1905	100	1	2	2
886	*Guatteria*	*oligocarpa*	Martius, C.F.P. von	714	S	14/01/1905	100	1	1	2
898	*Guatteria*	*latisepala*	Lehmann, F.C.	K27	S	20/03/1905	100	0	0	2
908	*Guatteria*	*hookeri*	Gardner, G.	306	S	11/01/1905	100	0	0	2
917	*Guatteria*	*dielsiana* (*G. ucayaliana* Diels.)	Tessmann, G.	3212	S	06/04/1905	100	0	0	2
874	*Guatteria*	*spectabilis*	Tessmann, G.	3235	S	06/04/1905	100	1	0	1
903	*Guatteria*	*modesta*	Tessmann, G.	3476	S	06/04/1905	100	0	0	1
921	*Guatteria*	*chlorantha*	Tessmann, G.	3423	S	06/04/1905	100	0	0	1
922	*Guatteria*	*calliantha*	Tessmann, G.	5764	S	07/04/1905	100	0	0	1
930	*Guatteria*	*candolleana*	Dusén, P.	1939	S	12/03/1902	103	1	?	?
905	*Guatteria*	*mosenii*	Mosén, C.W.H.	4002	S	15/12/1875	130	1	1	3
909	*Guatteria*	*hilariana* var. *verruculosa*	Mosén, C.W.H.	3337	S	25/01/1875	130	1	2	2
904	*Guatteria*	*moralesii*	Wright, C.	1851	S	1860-1864	141	1	2	3
872	*Guatteria*	*sordida* var. *ovalis*	Riedel, L.	1689	S	01/11/1833	168	1	2	2
871	*Guatteria*	*sordida* var. *lancifolia*	Riedel, L.	1689	S	01/11/1833	168	1	2	1
932	*Guatteria*	*psilopus*	Riedel, L.	1172	S	01/11/1832	173	0	0	?
895	*Guatteria*	*rigida*	Riedel, L.	438	S	01/08/1826	179	0	0	1
879	*Guatteria*	*umbrosa*	Riedel, L.	s.n.	S	01/10/1823	182	1	0 @	2
894	*Guatteria*	*riedeliana*	Riedel, L.	424	S	01/11/1821	184	0	0	1

Table 4. *Zehneria* voucher information, age, ng/ µl DNA extracted, DNA extraction success (0=no result; 1=successful extraction) and amplification success (*ssr1* and/or *trnL-F* and/or *gpd*) 2=all markers amplified).

Zehneria extraction number	**Genus**	**Species**	**Collector**	**Collection number**	**Herbarium**	**Collection date**	**Age (Absolute)**	**Success in extraction**	**ng/ µl DNA extracted**	**Successfull amplification**
Z-84	*Baijana*	*borneensis*	SAN	144787	L	2003	3	1	18.7	1
Z-44	*Neoachmandra*	*leucocarpa*	de Wilde	22281	L	26/07/2002	4	1	30.6	2
Z-49	*Diplocyclos*	*palmatus*	de Wilde	22200	L	26/07/2002	4	1	98.6	2
Z-50	*Cyclanthera*	*explodens*	de Wilde	22276	L	26/07/2002	4	1	73.3	2
Z-51	*Indomelothria*	sp.	de Wilde	22271	L	19/07/2002	4	1	34.9	2
Z-52	*Zehneria*	*mucronata*	de Wilde	22272	L	21/07/2002	4	1	4.1	1
Z-19	*Zehneria*	*scabra*	Oijen	75	Wag	17/05/2001	5	1	107	2
Z-29	*Indomelothria*	sp. nov.	Postar	SAN 143729	L	16/07/2001	5	1	3.7	1
Z-46	*Scopellaria*	cf *diversifolia*	de Wilde	SAN143748	L	17/07/2001	5	1	17.5	1
Z-87	*Borneosicyos*	*simplex*	SAN	144261	L	2001	5	1	45.7	1
Z-21	*Melothria*	*pendula*	Postar	SAN 141901	L	05/01/2000	6	1	9.5	1
Z-23	*Mukia*	*javanica*	de Wilde	SAN 141930	L	13/01/2000	6	1	7.8	2
Z-43	*Scopellaria*	*marginata*	de Wilde	SAN141903	L	05/01/2000	6	1	12.5	2
Z-45	*Neoachmandra*	*wallichii*	de Wilde	22149	L	25/08/2000	6	1	77.9	2
Z-28	*Neoachmandra*	*mesophila*	de Wilde	21935	L	15/02/1998	8	1	34.4	2
Z-71	*Urceodiscus*	*scabridula*	Sands	7143	L	1998	8	1	129.25	2
Z-76	*Zehneria*	*erythrocarpa*	Hidija	6961	L	1998	8	1	53.08	1
Z-38	*Urceodiscus*	sp.	G Weblen	1020	L	23/07/1997	9	1	21.2	1
Z-41	*Zehneria*	*indica*	Yamazaki	6639	L	27/09/1997	9	1	78.6	2
Z-12	*Mukia*	*maderaspatana*	Jongkind	3111	Wag	26/09/1996	10	1	149	2
Z-14	*Neoachmandra*	*cappilacea*	Jongkind	2447	Wag	1995	11	1	40	2
Z-22	*Mukia*	*celebica*	de Wilde	21757	L	14/01/1995	11	1	15.3	2
Z-27	*Scopellaria*	*marginata*	de Wilde	21794	L	19/02/1995	11	1	19.4	2
Z-82	*Coccinia*	*grandis*	de Wilde	21717	L	1995	11	1	35.3	2
Z-15	*Neoachmandra*	*gilleti*	de Wilde	11246	Wag	30/11/1994	12	1	175.6	2
Z-42	*Zehneria*	*mucronata*	de Wilde	21682	L	19/12/1994	12	1	50	2
Z-83	*Lageneria*	sp.	de Wilde	21664	L	1994	12	1	302.7	2
Z-85	*Citrullus*	*lunatus*	de Wilde	21686	L	1994	12	1	139.8	2
Z-35	*Zehneria*	sp.	Reynoso	7805	L	27/03/1993	13	1	3.8	1
Z-17	*Zehneria*	*marlothii*	Breteler	11695	Wag	03/11/1992	14	1	102.9	2
Z-86	*Benincasa*	*hispida*	Maxwell	91-924	L	1991	15	1	8.0	1
Z-47	*Zehneria*	sp.	S Griffith	s.n.	L	18/03/1990	16	1	84	1
Z-16	*Zehneria*	*keayana*	Carralho	4056	Wag	10/07/1989	17	1	63.4	2
Z-18	*Zehneria*	*minutiflora*	Rwaburindore	2824	Wag	31/07/1989	17	1	-	1
Z-25	*Zehneria*	cf. *emirensis*	Barnett	354	L	15/06/1985	21	1	24.6	2
Z-75	*Zehneria*	*pedicellata*	Vinas	4871	L	1981	25	1	18.51	1
Z-24	*Solena*	*heterophylla*	Larsen	34173	L	05/09/1974	32	1	101.3	1
Z-74	*Zehneria*	*grayana*	Powell	1351	L	05/05/1972	34	0	6.31	0
Z-48	*Zehneria*	aff *baueriana*	Chew Wee Lek	193	L	28/08/1971	35	1	8.8	1
Z-13	*Oreosyce*	*africana*	Friis	136	Wag	07/11/1970	36	1	45.3	1
Z-11	*Melothria*	*guadalupensis*	Groenendijk	26	Wag	17/01/1968	38	1	11.7	1
Z-53	*Cucumis*	*melo*	Herb. Wight	1145	L	1866-68	38	1	15.3	1
Z-80	*Peponium*	*sublittorale*	Grublet	1372	L	1968	38	1	15.52	1
Z-34	*Neoachmandra*	*filipes*	JM Wheeler	5839	L	01/10/1966	40	1	79.4	1
Z-36	*Neoachmandra*	*samoensis*	WR Sykes	170278	L	10/06/1965	41	1	174.3	2
Z-77	*Zehneria*	*pisifera*	Flenley	2185	L	15/12/1964	42	1	157.66	1
Z-26	*Neoachmandra*	*hallii*	Oldeman	366	L	26/08/1963	43	1	28.9	2
Z-33	*Melothria*	sp.	W&M Vink	15396	L	13/03/1962	44	0	43.6	0
Z-81	*Dactyliandra*	*welwitschii*	Nair	24973	L	1962	44	1	5.48	2
Z-32	*Zehneria*	sp.	Hoogland	7537	L	22/08/1960	46	1	102.5	2
Z-70	*Urceodiscus*	*belansis*	Hoogland	6798	L	28/06/1960	46	1	53.59	2

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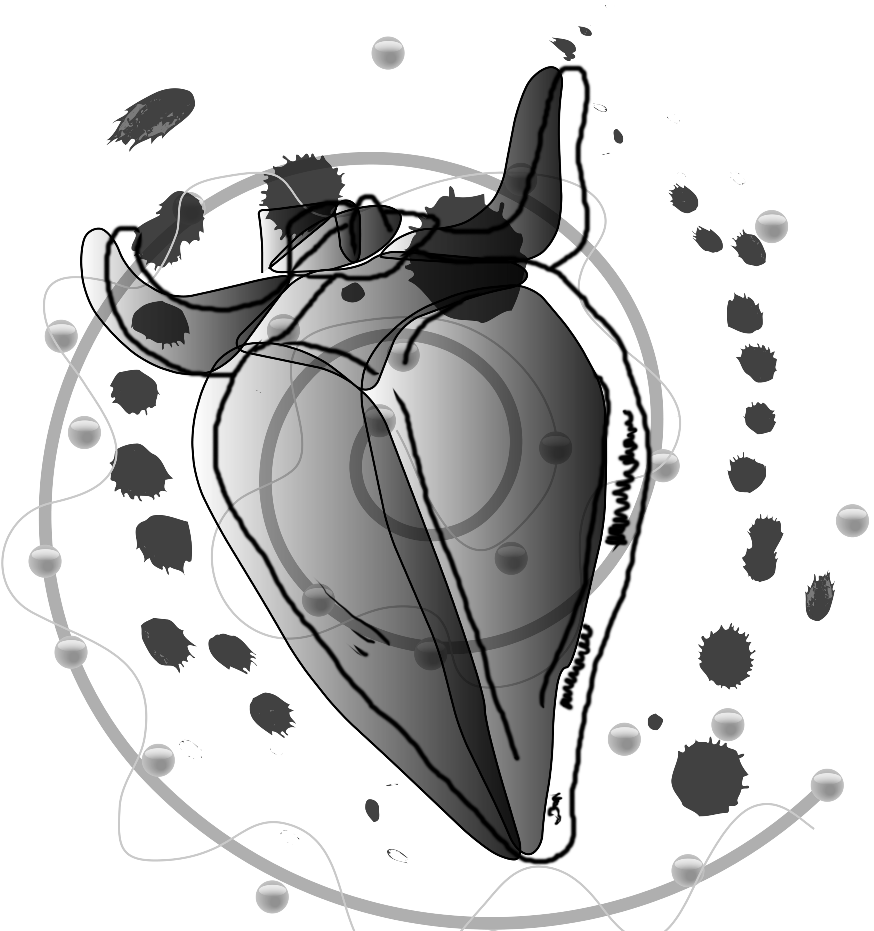
Z-78	*Trochomeria*	*macrocarpa*	Seydel	1353	L	1958	48	1	9	1
Z-31	*Neoachmandra*	*affinis*	L.J. Brass	23914	L	1953	49	1	77.6	1
Z-79	*Cucumella*	*aspera*	Seydel	563	L	1955	51	1	144.71	2
Z-20	*Neoachmandra*	*thwaitesii*	-	s.n.	Wag	14/11/1950	56	1	17.1	1
Z-72	*Zehneria*	*neocaledonica*	Gurillanimi	8895	L	1950	56	1	19.33	2
Z-73	*Zehneria*	*baueriana*	Guill	10315	L	1950	56	1	69.9	1
Z-89	*Raphidocystis*	*brachypoda*	Herb Lug. Bat	939.70.84	L	1938	68	0	3.53	0
Z-37	*Neoachmandra*	*pentaphylla*	AV Daniker	1174	L	10/02/1925	81	1	11.8	1
Z-39	*Zehneria*	*parvifolia*	-	s.n.	Wag	11/02/1898	108	1	23.2	1
Z-92	*Melothria*	sp.	Herb Lug. Bat	901.288-316	L	1887	119	1	2.25	1
Z-54	*Cucumis*	*melo*	Herb Lug. Bat	901.288-58	L	1818	188	1	17.4	1
Z-90	*Diplocyclos*	*palmatus*	Herb Lug. Bat	909.7-164	L	1766	240	0	5.21	0



8 DISCUSSION

SUMMARIZING AND COMBINING THE RESULTS

The phylogenetic part of this thesis has focused on the four main aims of the *Guatteria* project: (1) to clarify the phylogenetic position of the *Guatteria* group as a whole in the Annonaceae phylogeny, (2) to elucidate the relationships among the genera in the *Guatteria* group, (3) to produce a phylogenetic tree containing at least half the number of species of *Guatteria*, based on multiple sequences of the plastid genome, and (4) to provide insight into the evolution of key morphological and anatomical characters by character mapping onto the phylogenetic tree.

The phylogenetic position of the *Guatteria* group as a whole in the Annonaceae phylogeny has still not completely been determined (chapter 2). Although almost all relationships between the genera of the Long Branch Clade of Annonaceae could be elucidated, one uncertainty remains. The phylogenetic position of the *Guatteria* group, a clade containing the *Duguetia* group and the *Xylopia*-*Artabotrys*-clade could not unambiguously be determined. Interestingly, *Guatteria* as well as *Artabotrys* were also insecurely placed in morphological analyses (Doyle & Le Thomas, 1996) and it seems that neither molecules nor morphology are so far able to provide definitive insight in the phylogenetic position of (at least) *Guatteria*.

The relationships among the genera of the *Guatteria* group are much clearer now. In chapter 5 it is shown that *Guatteriopsis*, *Guatteriella* and *Heteropetalum* should be submerged into *Guatteria*. *Heteropetalum* could be put into its own subgenus because of its aberrant morphology and *Guatteriopsis* and *Guatteriella* might be given sectional status. However, the latter decision is impeded by a lack of phylogenetic resolution. Even though a phylogenetic tree containing c. 40% of the species of the *Guatteria* group was constructed on the basis of four regions of the plastid genome, supported resolution in this tree proved to be disappointing. Therefore, a completely new subgeneric classification of *Guatteria* would be premature because of the lack of molecular and morphological synapomorphies to define new sections (chapter 5). However, with regard to the currently recognised sections it can be concluded that most of them are probably non-monophyletic.

In chapter 5, all moderate to strongly supported clades in *Guatteria* (based on bootstrap as well as Bayesian posterior probabilities) were compared with the sections described by Fries, in order to evaluate the monophyly of these sections. Here, several other sections will be shortly looked at and some very preliminary conclusions are drawn.

Fries described several monotypic sections. The sections *Dichrophyllum* (*G. discolor*) and *Stigmatophyllum* (*G. puncticulata*) were sampled in this study but did not arise as distinct

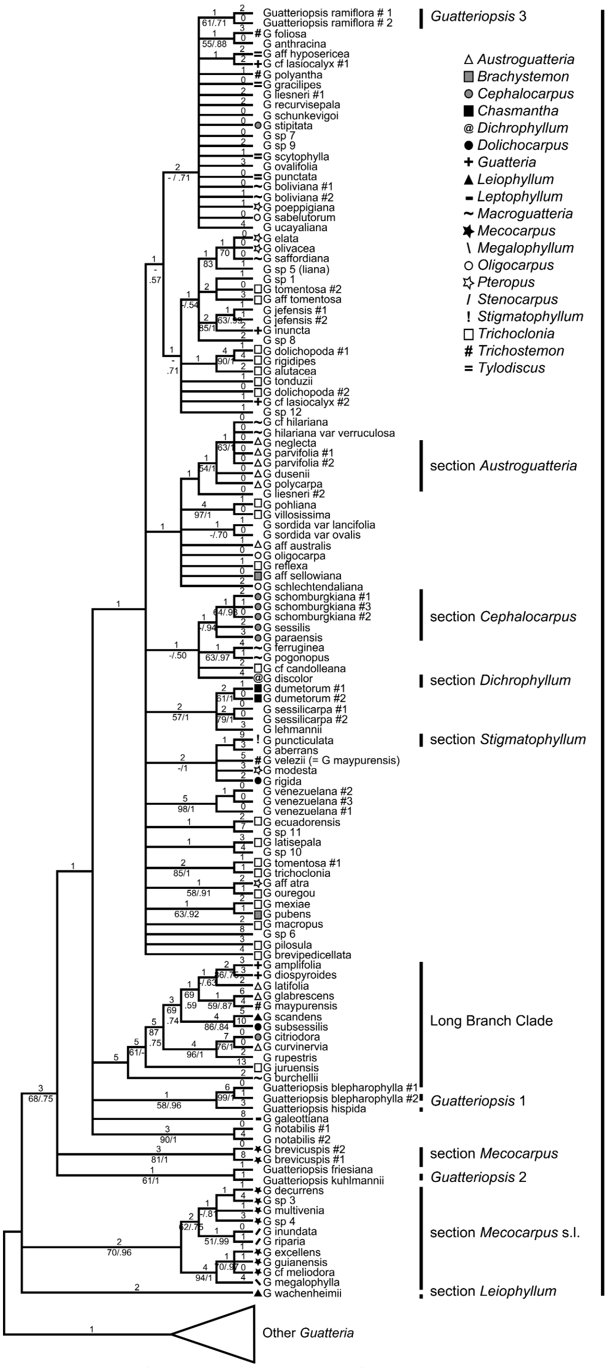


Figure 1. close up of South American Clade of *Guatteria* as discussed in chapter 5 of this thesis. Branch lengths are shown above the branches, bootstrap percentages and Bayesian posterior probabilities below. Sections discussed in text are indicated before the species names. Species without a symbol were never assigned to a section.

lineages (figure 1), thus so far not validating their monotypic section status. *G. discolor* is easily recognisable by its leathery, two-coloured leaves with a dense reddish brown indument on the lower side, and by quite large, shortly stipitate monocarps. However, it can morphologically easily be connected to species of section *Cephalocarpus*. This relationship is suggested by the molecular data as well, although the clade to which species of the sections *Cephalocarpus* and *Dichrophyllum* belong is only weakly supported (Bootstrap support (BS) absent; Posterior probability (PP) 0.5). *G. puncticulata* is nested in a clade that is only supported by Bayesian support (PP 1).

Section *Tylodiscus* is a section of which Fries stated that it might be a rather natural group that is spread throughout the Amazon region (Fries, 1939). So far, all species sampled in this study belong to a weakly supported clade (BS absent; PP 0.71) and within this clade resolution is completely absent (figure 1).

A section that so far does not prove to be monophyletic is section *Trichoclonia*. In this section very different species are united but many transitions between these species exist. One of the characteristics delimiting this section are the long erect hairs, covering the whole plant. This indument is very easily recognisable and unidentified specimens are therefore often assigned to this section as aff. *trichoclonia* (or aff. *tomentosa*; the oldest name in the section). However, it seems that this indument type shows a high level of homoplasy because the species of this section occur spread throughout the tree (figure 1). Therefore, this homoplastic complex-delimiting character should probably be discarded. This situation is comparable to the problematic use of the impressed secondary venation as a delimiting character for the *Guatteria amplifolia*-complex in Central America (chapter 6). *G. pohliana* was first described in a monotypic section (*Microphyllum*) by Fries (1939). At that time he wrote that this species showed affinity to section *Austroguatteria*. In his 1959 revision (Fries, 1959b) he merged both sections in section *Trichoclonia.* Indeed, *G. pohliana* clusters with a species from this section (*G. villossissima*; BS 97%; PP 1) but their relationships to the other species of section *Trichoclonia* remains unclear (figure 1).

Section *Cephalocarpus* consists of species that form very difficult species complexes and that occur mainly in the Amazon basin and Guiana. The section seems monophyletic (figure 1; BS absent; PP 0.94) except for *G. citriodora* and *G. stipitata*. *G. stipitata* is morphologically different from the other species in the section because of its stipitate monocarps and might be erroneously assigned to this section to begin with.

Finally, species from section *Austroguatteria* seem to be monophyletic (figure 1; BS 54%, PP 1.0). This is a section of which Fries mentions that it might be a natural one, partly on the basis of its Southeastern Brazilian occurrence. Most of the species form a weakly supported clade suggesting a natural grouping, only *G. curvinervia* falls outside. This species keys out together with *G. salicifolia* in Fries' treatment. *G. salicifolia* is morphologically somewhat isolated (Fries, 1939) and perhaps should be kept aside. It might therefore be true that *G. salicifolia* and *G. curvinervia* are inaccurately placed in this section in the first place.

The remaining sections (*Brachystemon*, *Guatteria*, *Leptophyllum*, *Macroguatteria*, *Oligocarpus*, *Pteropus*, *Sclerophyllum* and *Trichostemon*).do not seem to be monophyletic but based on the data at hand it is not achievable to draw any conclusion about these sections

One clade (BS 57%; PP 1) deserves a closer examination. The morphologically very different species *G. dumetorum*, (Panama), *G. sessilicarpa* (Panama) and *G. lehmannii* (Antioquia, Colombia) are united by several molecular synapomorphies, including a six base pair deletion in the plastid *trnE-F* region. There are at this moment no obvious morphological characters to unite these species.

Table 1 summarises the results of the section evaluation of this chapter and of chapter 5. An indication is given if a section is thought to be (possibly) monophyletic or not. Most sections should probably not be used because of their polyphyletic constitution but more data are needed to substantiate this claim.

Table 1. Preliminary conclusions on the status of Fries' 1959 sections. It is indicated if sections are so far found to be (mainly) monophyletic, possibly monophyletic, not monophyletic, or conclusion not drawn (?).

Subgenus	**Section:**	**Status:**
Anomalantha	Anomalantha	monophyletic; distinct lineage
Guatteria	Austroguatteria	possibly monophyletic
Guatteria	Brachystemon	?
Guatteria	Cephalocarpus	monophyletic
Guatteria	Chasmantha	mainly monophyletic
Guatteria	Cordylocarpus	?
Guatteria	Dichrophyllum	not a distinct lineage
Guatteria	Dimorphopetalum	?
Guatteria	Dolichocarpus	not monophyletic
Guatteria	Guatteria	?
Guatteria	Leiophyllum	not monophyletic
Guatteria	Leptophyllum	?
Guatteria	Macroguatteria	?
Guatteria	Mecocarpus	mainly monophyletic
Guatteria	Megalophyllum	not a distinct lineage
Guatteria	Oligocarpus	?
Guatteria	Pteropus	?
Guatteria	Sclerophyllum	?
Guatteria	Stenocarpus	monophyletic
Guatteria	Stigmatophyllum	not a distinct lineage
Guatteria	Trichoclonia	?
Guatteria	Trichostemon	?
Guatteria	Tylodiscus	possibly monophyletic

The interesting question is what caused the lack of resolution in the phylogenetic tree of *Guatteria*. In chapter 4, three major biogeographical events in the history of the genus were reconstructed and hypothesised to be responsible for the pattern found. It is thought that a trans-oceanic Miocene migration from Central into South America has taken place before the closing of the Isthmus of Panama, followed by a major diversification of the lineage within South America. Such a rapid and recent burst of diversification from the most recent common ancestor of the extant species, has already been shown to result in poorly resolved phylogenies (Richardson & al., 2001a). The third important biogeographical event was the re-migration of several South American lineages into Central America via the closed Panamanian land bridge. Therefore, it can be concluded that *Guatteria* is not an Amazonian centred genus *sensu* Gentry but a major Miocene radiation that followed its dispersal into South America. This phylogenetic pattern is comparable to that found in *Ocotea* (Lauraceae; Chanderbali & al., 2001). A closer comparison between the three largest Neotropical genera that mainly comprise trees (*Guatteria*, *Ocotea* (Lauraceae) and *Inga* (Fabaceae) is therefore desirable.

This rapid diversification of the "South American Clade" within *Guatteria* (chapter 4) has lead to a large amount of species. As was shown in chapter 3, however, *Guatteria* itself does not constitute a radiation. *Guatteria* is in itself a large genus, but not larger than can be explained on the basis of stochasticity. As a matter of fact, none of the largest genera in the family are the result of radiations (except for *Goniothalamus*). The larger clades within Annonaceae probably did not result from intrinsic key-innovations that significantly influenced the rate of diversification within the family. Because of the geographic structure in some parts of the tree, a number of clades might be species-rich as the result of a radiation after a founder event. It has already been suggested that moderately low rates of dispersal (low enough to interrupt gene flow, but high enough to allow the occasional colonization of new habitats) can result in the highest rates of speciation (Givnish & Systma, 1997). The diversification pattern in *Guatteria* might be caused by adaptation to a number of different ecological niches by changes in vegetative characters (Morawetz & Waha, 1985) or its populations might have been subdivided on a regular basis due to abiotic factors. In the latter case no one character or set of characters would be causally involved in promoting speciation (Cracraft, 1985).

The recent divergence of *Guatteria,* the lack of phylogenetic structure and the absence of (key-)characters associated with speciation severely hampered character mapping onto the phylogenetic tree. Some characters have been looked at (e.g. wood anatomical characters, chapter 5) but the evolution of most characters is still poorly understood. In order to gain further insight into the evolution of certain characters the *Guatteria amplifolia*-complex (the most problematic complex of *Guatteria* species in Central America) was looked at. Such species complexes can prove to be an excellent opportunity to study the patterns of evolution of characters associated with speciation. However, it was found that most accessions of the monophyletic complex could not be separated into well differentiated clades on the basis of the molecular data at hand. This lack of genetic divergence might be found in the recent common genetic history of the complex (chapter 4) or ongoing hybridization (chapter 6). It was shown that the use of a homoplastic complex-delimiting character (impressed secondary leaf venation) is unwise, as was mentioned above for the use of the “hairs” of section *Trichoclonia*. More insight into the complex morphology of the genus will probably be postponed until more insight has been gained into the phylogenetic relationships among the species.

GATHERING MORE DATA: INCREASING PHYLOGENETIC RESOLUTION

These are exciting times. The amount of genome information is increasing at an unprecedented pace and sequencing becomes ever more rapid and inexpensive (Margulies & al., 2005). Increased resolution in the phylogeny of *Guatteria* can therefore probably be achieved by sequencing additional gene regions at low costs. Furthermore, whole-genome data for a large number of organisms are rapidly expanding (Liolios & al., 2006), and the first complete genome of a tree (*Populus trichocarpa*) has recently been sequenced (Tuskan & al., 2006). Comparison of these whole-genome sequences on a large evolutionary time scale can offer insights into the macroevolutionary pattern of genome evolution. By selecting more closely related groups (that diverged less than 20 million years ago) it might be possible to understand processes of genome evolution that are not apparent from more distant comparisons. At an microevolutionary scale (less than 500,000 years) genomic data can be a rich data source for population genomic studies and help to understand intraspecific patterns of genome evolution (Jackson & al., 2006). So far in Annonaceae research, only sequence data of plastid DNA regions have been used. These data have one major draw-back: only four states per character are possible. Reconstruction of deeper nodes in the tree (such as the polytomy in the Long Branch Clade of Annonaceae; chapter 2) or clades in the tree with short branches (Short Branch Clade and Miliusoids; Mols & al., 2004; Pirie & al., 2006) may fail. In the future new genomic characters, like plastomes (full sequences of the plastid genome) might contribute to the elucidation these relationships. Also, characters above sequence level, such as chloroplast gene rearrangements (inversions, tandem repeats), chloroplast gene indels (single, multiple or duplication via inclusion) and presence and absence of chloroplast gene introns prove to be an additional data resource (Wolf & al., 2004). Although targeted PCR and sequencing of selected orthologous genes is an obvious way to proceed, an alternative approach for data collection might be to sequence expressed sequence tags (ESTs; Philippe & Telford, 2006). The principle of EST sequencing is that a cDNA library is made from each organism of interest, from which a few thousand clones (i.e. ESTs) are sequenced and analysed using bioinformatics methods (Philippe & Telford, 2006).

In order to produce these genome data, the traditional Sanger sequencing method will probably be supplemented or replaced. Although this method has performed extremely well, it is not able to obtain increases in throughput and speed beyond those seen the last decades (Jackson & al., 2006). Several new sequencing techniques are able to sequence at increased speed and lower costs (Metzker, 2005). These new methods have two main advantages. They allow a single molecule to be used to generate many bases of sequences read, instead of the irreversible dideoxy termination of Sanger sequencing. Furthermore, the sequence is not represented by a ladder of differentially sized fragments and thus they can avoid electrophoretic steps to isolate and read the sequence (Jackson & al., 2006).

An increasing amount of studies report on "radiations," speciation events that cannot be reconstructed with the use of standard plastid markers (e.g. plastid markers in chapter 2). Next to the above mentioned structural data from whole-genome sequences, more variable markers should be sought. This is true for higher-level relationships as well as for the reconstruction of inter- and infraspecific relationships. Not only might it be necessary to use different taxonomic methods (molecules and morphology) for assessing species boundaries at these levels, but also genomic data from different genomes. In addition to the much used plastid genome, this can include data from the mitochondrial genome (Knoop, 2004) or from nuclear single-locus molecular markers (Crawford & Mort, 2004). Furthermore, much more differentiation in techniques should be applied, such as the usage of AFLP data, microsatellites or Inter Single Sequence Repeat (ISSR) markers, although the use of these multilocus markers for phylogenetic reconstruction has been much debated (e.g. Goldstein & Pollock, 1997; Koopman, 2005). Preferably, several sources of data should be used in conjunction. In this way sequence data can for instance be used to reconstruct the backbone of a phylogeny, while more variable (population genetic) markers are used to elucidate relationships at lower taxonomic levels (e.g. chapter 6; or Chatrou & al., in prep: "Microsatellite flanking regions boost plant species-level phylogenetics: the case of *Annona*").

With the generation of phylogenetic hypotheses at lower taxonomic levels (species and below) a new realm of biological phenomena possibly influences our phylogenetic inference. It has already been shown that metabolic rate, generation time and body size all can influence nucleotide substitution rate (Martin & Palumbi, 1993). The impact of other population genetic processes like "selective sweeps" (also called genetic hitch-hiking; Smith & Haigh, 1974) is less well understood. A selective sweep occurs when a new mutant rises in frequency by selection, and adjacent chromosomal regions are also swept to fixation. This leads to regions of low nucleotide diversity (e.g. documented for humans: Diller & al., 2002; and extensively for Drosophila: e.g. Derome & al., 2004). Furthermore, better understanding of processes like "C to U RNA-editing" (where alternative protein products are generated from a single structural gene) might change our perception of the link between genotype and phenotype. This in turn can help us to understand a phenomenon like homoplasy and the ease with which it can occur. It has already been shown that C to U RNA-editing is important for amplifying mammalian genetic diversity in a regulated manner (Blanc & Davidson, 2003) but how this influences phylogenetic reconstruction is not known.

With the increase of genomic data it has also become increasingly clear that there is much more genetic variation within populations than realised before (Bachmann, 2001). The dynamics of genetic diversity should be studied better, in order to understand the effects of these processes on speciation. A young and rapidly growing field that is incorporating data from genealogical and phylogeographical scales is phylogeography (Avise, 2000). It studies the spatial relationships of such genealogies and analyses these to deduce the evolutionary history of populations, subspecies and species. It is precisely at these levels that the process of speciation occurs (Templeton, 2001). Understanding the relationships between groups of organisms at such a fundamental level will help us to understand the process of cladogenesis. Ultimately, this will contribute to a better understanding on how to reconstruct the tree of life. Phylogeography might prove to be the link between two so far almost completely separated fields in biology, population biology and molecular systematics. Insights from this emerging field will surely alter our view on evolution.

Gathering more genomic data will become increasingly easier but this does not mean that proper taxon sampling should be neglected. Ideally all the species in a higher group, such as a genus, should be sampled to ensure that those species reflect evolutionary entities within the group. In this way the effects of other processes, such as extinction, can be ruled out as explanations for observed patterns (Barraclough & Nee, 2001). (A combination of) genomic regions that provide sufficient signal without compromising taxon representation is therefore essential for accurate assessment of evolutionary histories (Soltis & al., 2004). Finding the minimum amount of data necessary to adequately reconstruct phylogenetic relationships is non-trivial because insufficient data can lead to situations were truly independent (homoplasious) substitutions are treated as historical signal, even when taxon sampling is dense (Hillis, 1996; Chase & al., 2006)

ANALYSING THE DATA: A FREQUENTIST OR BAYESIAN APPROACH

Collecting data, being sequences, whole genomes information, or morphological characters, is only the first step in a phylogenetic study. Several components minimally make up a phylogenetic analysis (Leebens-Mack & al., 2006), an important component being the construction of a tree based on the gathered data. Hopefully (but not probably), this tree reflects the true phylogeny of the group under study. When searching for such "best" trees, several approaches can be used, as explained in chapter 1. After tree estimation, statistical support for the phylogenetic hypothesis at hand is calculated. For this, the preferred method is highly dependent on the researcher's interpretation of probability (where probability is the measure of uncertainty). With or without knowing, the researcher adheres to one or several very different statistical schools: frequentist, Bayesian or Fisherian. In the frequentist approach, relative frequencies are looked at, usually via the repeated sampling principle. In the Bayesian approach, the measure of the degree of belief that an event will occur is expressed. The Fisherian approach is likelihood based and the probability of the observed data as a function of a statistical model is looked at. All three schools have fundamentally different views of probability and these different views are the source of much debate. In this thesis, a frequentist and Bayesian approach was used.

An example of the frequentist approach to phylogeny reconstruction is the bootstrap method. In bootstrapping the original data matrix is randomly re-sampled with replacement to produce pseudo-replicate data sets. After this the tree-building algorithm is performed on each of the replicate data sets. This method only contains minimal assumptions (sites should be independent, data are not supposed to be normally distributed) but can be a computational burden. Bootstrapping offers a measure of which parts of the tree are weakly supported. A grouping that is present in a low percentage of the bootstrap replicates is sensitive to for instance the exact combination of sites that were sequenced. This implies that if another data set were collected, there is a good chance that the group would not be recovered. Bootstrap values help to predict whether the same result would be attained if more data were collected (i.e. it helps to assess the effects on tree construction of variability within the sequences), not whether the obtained result is correct (Holder & Lewis, 2003). Furthermore, bootstrapping says nothing about the fundamental soundness of the method by which we choose a tree; it only indicates how variability in the data affects the outcome of the method (Allman & Rhodes, 2004). Therefore, high bootstrap values are a necessary, but not sufficient, condition for having high confidence in a group.

Bayesian analyses are useful because they allow complex models of sequence evolution to be implemented and the primary analysis produces both a tree estimate and measures of uncertainty for the groups on the tree (Holder & Lewis, 2003). The essence of the Bayesian viewpoint is that there is no logical distinction between model parameters and data. Data are observed variables and parameters are unobserved variables. Their joint distribution is a product of the likelihood and the prior (Beaumont & Rannala, 2004). The likelihood is a conditional distribution that specifies the probability of the observed data given any particular values for the parameters and is based on a model of the underlying process. Prior probabilities of different hypothesis convey the scientist's beliefs before having seen the data (Holder & Lewis, 2003) and encapsulates information about the values of a parameter before examining the data in the form of a probability distribution (Beaumont & Rannala, 2004). Together these two functions combine all available information about the parameters (Beaumont & Rannala, 2004). The main aim of Bayesian inference is to calculate the posterior distribution of the parameters, which is the conditional distribution of parameters given the data (i.e. the probability ("p") given the data we have observed). The optimal hypothesis is the one that maximizes the posterior probability. In tree estimation it can be very practical to use a Bayesian method, especially when a probability model includes many interdependent variables that are constrained to a particular range of values (Beaumont & Rannala, 2004). Furthermore, the method yields easy support values since no approximations have to be made.

A potentially attractive feature of Bayesian analysis is the ability to incorporate background information into the specification of the model (Beaumont & Rannala, 2004). However, the concept of prior probabilities causes much controversy between the frequentist and Bayesian schools of statistics. Researchers are often uncomfortable with specifying prior distributions for all parameters because they find them too subjective (Holder & Lewis, 2003). Bayesian analyses often begin with very vague or even flat priors (all outcomes are equiprobable) and then move toward more informative priors as researchers become more comfortable with the effects of modifying the prior (Lewis, 2000). There are several ways to specify a prior, for instance the posterior probability (or other information) of a primary search can serve as a prior probability of the next. Also non-parametric bootstrap estimates can be used as a starting point in order to reduce subjectivity in the estimation of the prior. Bayesian methods can prove to be an excellent tool in evolutionary research because often prior knowledge is at hand, which can be incorporated into the analyses. This knowledge can have many forms, such as information on morphology, anatomy, karyology, chemistry, etc. In the frequentist approach all tree estimates are seen as independent. In a Bayesian framework, background knowledge (the prior) is always updated when new information accumulates.

Another difference with the frequentist approach is the fact that the algorithm used in a Bayesian analysis does not attempt to find the highest point in the space of all parameters (e.g. the shortest tree in tree space). Bayesian analysis uses the Markov chain Monte Carlo (MCMC) algorithm for approximating probability distributions. MCMC takes a series of steps and at each step a new location in parameter space is proposed as the next link in a chain. This proposed location is usually similar to the present one because it is generated by the random pertuberation of a few of the parameters in the present state of the chain. As a next step the relative posterior probability density at the new location is calculated. If the proposed location has a higher posterior probability density than that of the present location of the chain, the move is accepted. This new location becomes the next link in the chain and the cycle is repeated (Holder & Lewis, 2003). If the posterior probability of the new location is lower, it can still be accepted, but only a proportion of the time. Small steps downward are accepted often, whereas big leaps downward are discouraged. If the new location is rejected the present location is used as the next link in the chain (and the last two links are identical; Holder & Lewis, 2003). By repeating this procedure for instance 1,000,000 times, a long chain of links in parameter space is created. The product of the specified model and prior distribution are integrated over all possible parameter values to determine the posterior probability for each tree (Holder & Lewis, 2003). Assessing whether or not the chain has run long enough to provide reliable estimates of the posterior probability is a crucial issue when using MCMC.

Choosing among available methods for tree estimation and support can be complex because many more exist than discussed here (e.g. Shi & al., 2005). All methods have their advantages and disadvantages and so far no general standard as how to do a phylogenetic analysis exist. In response to this, a minimum reporting standard has been proposed, in order to be able to compare and evaluate the analyses done (Leebens-Mack & al., 2006).
With regard to the methods used here, it can be mentioned that parsimony has been reported as more conservative than Bayesian analyses, in that it resolved fewer incorrect clades (Simmons & al., 2006). It was furthermore shown that Bayesian analysis can lead to more posterior probabilities in the 0.85-1 range than is expected from theory (Cummings & al., 2003). This means that Bayesian statistics can overestimate support for particular nodes on a tree (Simmons & al., 2004). A bootstrap approach might be less prone to strongly supporting a false phylogenetic hypothesis (Douady & al., 2003). This effect might be illustrated by figure 2 in chapter 4. Although bootstrap support is absent for most nodes in

the backbone of the tree, Bayesian posterior probabilities show moderate to even strong support. A more conservative parsimony analysis in combination with for instance bootstrap might therefore be preferable. On the other hand, it has been shown that Bayesian analysis can provide high support values for correct clades with fewer characters than needed for bootstrap (Alfaro & al., 2003). Additionally, as a model for studying molecular evolution, parsimony is inadequate (Yang, 1996; Voronov & al., 1998) because it cannot incorporate models to account for different aspects of the heterogeneity in the evolutionary process of different genes that are known to exist.

All tree-building methods are known to converge on the same topology when sufficient evidence is available (Hillis, 1996). As discussed above, with the increasing speed at which genomic data becomes available, producing sufficient (genomic) data will no longer be a limiting factor in the near future. As a result, thorough analysis of this data will become ever more important and complex. However, the discussion on the choice for the most appropriate method of analysis will for sure not cease. As explained above, this is partially the result from the fact that methods from different statistical schools (and thus with different properties) are compared. Both posterior probabilities and bootstrap supports are of great interest for phylogenetic reconstruction as potential upper and lower bounds of node reliability, but they are surely not interchangeable and cannot be directly compared (Douady & al., 2003). Therefore, preference of the researcher and his (statistical) view on the world will stay decisive in selecting methods for tree estimation and support.

EXPLAINING THE RESULTS: SYSTEMATICS AS A PREREQUISITE

Traditionally, the core of systematics is a description of each species and a means of distinguishing among them; to this core has relatively recent been added the exercise of resolving their evolutionary relationships (Godfray, 2002). These relationships are mostly depicted by a (phylogenetic) tree. Such a tree in itself is meaningless, it is only a researcher's tool to learn something about observed biological phenomena and an aid for explaining these. For plant systematists, this means after the lab-work has been done, they have to return to their voucher specimens. This material is essential for investigating the phylogenetic patterns observed from a tree. The voucher specimens (and usually many more unsampled specimens that need to be studied) are stored in a herbarium.

After the first World Summit on Sustainable Development in Rio de Janeiro it seemed that herbaria entered a time of growth and significance (Smith & al., 1996). This because it was realised that herbaria are huge warehouses of information on plant biodiversity (Smith, 2006). They provide the comparative material that is essential for studies in taxonomy, systematics, ecology, anatomy, morphology, conservation biology, biodiversity, ethnobotany, and paleobiology, as well as being used for teaching and by the public (Funk, 2003). The herbarium was invaluable for the molecular work done for this thesis because many herbarium specimens had to be used (see introduction). Herbaria are and increasingly will be important sources of DNA for systematic studies (see also chapter 7).

Strangely, fifteen years after the World Summit many natural history collections worldwide are being closed down or budgets are being cut (Dalton, 2003; Gropp, 2003), one of the most recent examples being the closure of one of the most modern (completely APG ordered) herbaria in the world, that of Utrecht. Although this herbarium was founded in 1816, being one of the oldest still existing research groups at Utrecht University, the collections will be moved to another (undetermined) institute and the staff is retiring or will be re-assigned. This means that no new generation of systematists can be trained at Utrecht University, a situation that has occurred at other universities as well (Gropp, 2003)

This may seem a trivial problem but many conservation, environmental, legal and other matters nowadays hinge on scientific names, including their status and thus on taxonomy (Scotland & al., 2003). The same is true for biology itself. Furthermore, biodiversity is a resource which can be tapped to enhance human welfare (Wilson, 2000; Scotland & al., 2003) but the question is who will have sufficient knowledge of this biodiversity to be able to tap it in the future.

For science itself, this negative trend is already visible. There are too few practising taxonomists around to assist molecular systematists to interpret their phylogenies and sensibly harmonise them with existing classification hypotheses or translate them into usable new classifications (Sanders & Judd, 2000; Smith, 2006). The gap between molecular systematists and taxonomists will widen as new generations of students receive less and less training in the full complement of systematic methods and systematic positions are filled by molecular biologists with little training beyond molecular laboratory techniques (Sanders & Judd, 2000). A good example of cooperation between taxonomists and molecular systematists is research on a species complex of problematic, cryptic Australian freshwater shrimp (Atyidae; Caridina). Here, resolved genetic groupings were validated with morphological characters and new insights were incorporated into “traditional taxonomy” by creating morphological keys that could accurately characterize the previously unappreciated level of genetic biodiversity (Page & al., 2005).

Modern systematic research uses theories and methods of several other scientific disciplines, which are in themselves highly complex. For this thesis for instance, time had to be divided between field-work to gather plant material, molecular laboratory work to gather sequence data, data analysis (based on complex mathematical models) and taxonomic work to learn the characteristics of the species under study. This project could be carried out because specialists were present that could quickly pass on information about each topic, in particular the necessary taxonomic knowledge. However, within a few years the taxonomic specialists will be retired, taking with them their vast body of knowledge. Unfortunately, most of this knowledge cannot be written down easily and can only be transferred by working along-side these specialists. Death of current day systematics and re-learning 250 years of knowledge in the future will take a disproportional investment (Godfray, 2002). Therefore permanent staff positions at universities have to be assigned to taxonomists in order to save taxonomic knowledge at a time when it is not too late.

Some perceive taxonomy as being in crisis because lacking prestige and resources are crippling the continuing cataloguing of biodiversity (Godfray, 2002), although others contradict this view (Scotland & al., 2003). One reason why taxonomy is not fashionable with policy makers, is that it scores low with regard to impact factors, mainly because it differs in its most basic dynamics of other sciences (reviewed in Ellis, 2002). Another reason is that descriptive taxonomy in itself does not generate new ideas for testing hypotheses. It does however facilitate many new areas of research. This can be compared to raw, unannotated DNA sequences that are unexciting and of relatively little value in themselves to non-specialists (Godfray, 2002). However, this “descriptive genomics” (as I will call it) does sound exciting and new, mainly because it involves molecular techniques and is thus perceived to be “real science.” As a result of this perception, much money is assigned to molecular work and within 10 or 20 years time it will be simpler to take an individual organism and get enough sequence data to assign it to a “sequence cluster” (or species) than to key it down using traditional methods (Godfray, 2002). Notwithstanding the tremendous advances in the understanding of the branching order of the tree of life, the overwhelming focus on phylogeny reconstruction has come at a cost: a lack of interest in the fundamental areas of species identification, description and classification (Scotland & al., 2003).

DNA taxonomy (with DNA barcoding as a subdiscipline) as well as web-based taxonomy are exciting, new and promising fields within systematics. However, cautiousness is required. These new advances should be treated as tools and not goals in their own right. An example of a fashionable, but scientific questionable project is the Moorea Biocode Project (Check, 2006). The aim of this project is to collect multiple genetic and ecological data about each species on Moorea (an island 15 km northwest of Tahiti). This information will be collected in linked databases and should give scientists more information than barcoding a single DNA sequence (Check, 2006). The results of such an endeavour are questionable and probably will contribute little extra in comparison to standing practice. The danger, however, lies in the fact that these projects, although scientifically questionable, might sound fashionable for funding agencies. Instead of investing in basic taxonomic knowledge, their money is directed towards fashionable descriptive genomics mega projects. In that way, databases are filled with DNA barcodes of plants at a time that no general (“gold”) standard for barcoding exists. A counter argument might be, that it will take a long time to develop such a standard and that with decreasing costs and time for sequencing, additional data can be gather fairly easy in the future. Nevertheless, applied properly DNA taxonomy can contribute greatly to our understanding of evolution (e.g. Gompert & al., 2006). Furthermore, it might make the Linnaean taxonomic system more accessible, with benefits to ecologists, conservationists, and a diversity of organisations that use biodiversity data (Hebert & Gregory, 2005). In the long run, it might even revolutionise the way taxonomy is being practiced.

The same is true for web-based taxonomy. Most taxonomic information is available in scientific journals, but copyright and high costs of subscriptions put this information beyond the reach of many in the developing world (home to >95% of species whose descriptions have been published; Falco, 2006). However, freely accessible, high quality taxonomic data available via the internet can dramatically alter the use of this knowledge. Unfortunately, only a relatively small amount of information is already available on the web and what is present are typically simple lists of little use to non-taxonomists (Falco, 2006). Digitising information and uploading it to websites with as ultimate goal an online lists of names or pictures, is therefore not enough. These websites should be designed in order to serve as tools for specialists as well as non-specialists, to quickly and easily find the information they need. Taxonomists should nowadays more than ever be aware of the end-users of their products. Only in this way can they maintain a healthy balance between basic taxonomic research and service delivery to non-specialists, as these days is required by universities and funding agencies (Smith, 2006).

LOOKING INTO THE FUTURE

The scope of the research on *Guatteria* so far has been fairly restricted. An overall preliminary phylogenetic classification, but no recent thorough taxonomic revision has been undertaken. Taxonomic knowledge of *Guatteria* is scattered between people and because of retirement and lack of fixed staff positions in the near future this knowledge might be lost. A complex group like *Guatteria* requires many years of study, and this surpasses the limited scope of a single PhD-project. Continuation of the *Guatteria*-project is highly desirable, especially since the same evolutionary patterns seem to exist in other plant groups as well (e.g. *Inga* and *Ocotea*). Furthermore, many of the questions that lay at the basis of this project still have not been answered in a definitive way.

With regard to *Guatteria* a first step has been taken towards more fully understanding the evolution of the genus. However, the lack of resolution in the phylogenetic tree make it clear that still a lot of work has to be done in order to really elucidate all phylogenetic relationships. Furthermore, a proper evaluation of morphological characters necessary to circumscribe problematic species, construction of a new classification and lastly a revision are still out of reach. Therefore, this thesis can only be ended by returning to Fries (1939) when he wrote: "*Dieser Versuch muss aber als ein Provisorium aufgefasst werden. Es erweist sich nähmlich, das die Gruppierung der Arten auf bedeutende Schwierigkeiten stösst.* [.....] *Umgruppierungen werden zweifellos nötig sein, wenn vollständiges Material zu Gebote stehen wird und wenn man auch über den systematischen Wert der Charaktere mehr Klarheit gewinnen kann, als es mir gelungen ist*".

REFERENCES

Aldrich, J., Cherney, B. W., Merlin, E. & Christopherson, L. 1988. The role of insertions/deletions in the evolution of the intergenic region between *psbA* and *trnH* in the chloroplast genome. *Cur. Genet.* 14: 137-147.

Alfaro, M. E., Zoller, S. & Lutzoni, F. 2003. Bayes or Bootstrap? A simulation study comparing the performance of Bayesian Markov Chain Monte Carlo Sampling and Bootstrapping in assessing phylogenetic confidence. *Mol. Biol. Evol.* 20: 255-266.

Allman, E. S. & Rhodes, J. A. 2004. *Mathematical models in Biology: an introduction*. Cambridge University Press, Cambridge, United Kingdom.

APG 1998. An ordinal classification for the families of flowering plants. *Ann. Missouri Bot. Gard.* 85: 531-553.

APG-II 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141: 399-436.

Armbruster, W. S., Debevec, E. M. & Willson, M. F. 2002. Evolution of syncarpy in angiosperms: theoretical and phylogenetic analyses of the effects of carpel fusion on offspring quantity and quality. *J. Evol. Biol.* 15: 657-672.

Aublet, F. 1775. *Histoire des plantes de la Guiane françoise*. Pierre-François Dodot jeune, London, Paris.

Avise, J. C. & Johns, G. C. 1999. Proposal for a standardized temporal scheme of biological classification for extant species. *Proc. Natl. Acad. Sci. USA* 96: 7358-7363.

Avise, J. C. 2000. *Phylogeography. The history and formation of species.* Harvard University Press, Cambridge, Massachusetts.

Bachmann, K. 2001. Evolution and the genetic analysis of populations: 1950-2000. *Taxon* 50: 7-45.

Backlund, A. & Bremer, K. 1998. To be or not to be - principles of classification and monotypic plant families. *Taxon* 47: 391-400.

Barraclough, T. G. & Nee, S. 2001. Phylogenetics and speciation. *Trends Ecol. Evol.* 16: 391-399.

Beatty, J. 1982. Classes and cladistics. *Syst. Zool.* 31: 25-34.

Beaumont, M. A. & Rannala, B. 2004. The Baysian revolution in genetics. *Nat. Rev. Gen.* 5: 251-261.

Beheregaray, L. B., Gibbs, J. P., Havill, N., Fritts, T. H., Powell, J. R. & Caccone, A. 2004. Giant tortoises are not so slow: rapid diversification and biogeographic consensus in the Gálapagos. *Proc. Natl. Acad. Sci. USA* 101: 6514-6519.

Bentham, G. 1860. Notes on Anonaceae. *J. Proc. Linn. Soc.* 5: 67-72.

Bermingham, E. & Martin, A. P. 1998. Comparative mtDNA phylogeography of neotropical freshwater fishes: testing shared history to infer the evolutionary landscape of Central America. *Molec. Ecol.* 7: 499-517.

Blanc, V. & Davidson, N. O. 2003. C-to-U RNA editing: mechanisms leading to genetic diversity. *J, Biol. Chem.* 278: 1395-1398.

Blanco, M. A., Whitten, W. M., Penneys, D. S., Williams, N. H., Neubig, K. M. & Endara, L. 2006. A simple and safe method for rapid drying of plant specimens using forced-air space heaters. *Selbyana* 27: 83-87.

Bridson, D. & Forman, L. 1992. *The herbarium handbook. Revised edition*. Royal Botanic Gardens Kew, United Kingdom.

Brooks, D. R. & McLennan, D. A. 2002. *The nature of diversity: an evolutionary voyage of discovery*. The University of Chicago Press, Chicago and London.

Bruns, T. D., White, T. J. & Taylor, F. M. 1991. Fungal molecular systematics. *Annu. Rev. Ecol. Syst.* 22: 525-564.

Bruns, T. D., Vilgalys, R., Barns, S. M., Gonzalez, D., Hibbett, D. S., Lane, D. J., Simon, L., Stickel, S., Szaro, T. M., Weisburg, W. G. & Sogin, M. L. 1992. Evolutionary relationships within the fungi: analyses of nuclear small subunit rRNA sequences. *Mol. Phyl. Evol.* 1: 231-241.

Buchwald, N. F. 1970. Robert E. Fries. Notitser (in Danish). *Friesia* 9: 348-354.

Burnham, R. J. & Graham, A. 1999. The history of Neotropical vegetation: new developments and status. *Ann. Missouri Bot. Gard.* 86: 546-589.

Bygrave, P. 2000. *Molecular Systematics of Annonaceae Juss. PhD Thesis*. Botany department, School of Plant Sciences, The University of Reading, UK.

Camin, J. H. & Sokal, R. R. 1965. A method for deducing branching sequences in phylogeny. *Evolution* 19: 311-326.

Chan, K. M. A. & Moore, B. R. 2002. Whole-tree methods for detecting differential diversification rates. *Syst. Biol.* 51: 855-865.

Chan, K. M. A. & Moore, B. R. 2005. SYMMETREE: whole-tree analysis of differential diversification rates. *Bioinf.* 21: 1709-1710.

Chanderbali, A. S., van der Werff, H. & Renner, S. S. 2001. Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. *Ann. Missouri Bot. Gard.* 88: 104-134.

Chanderbali, A. S. 2004. *Endlicheria* (Lauraceae). Pp. 141 in, *Flora Neotropica Monograph*, vol. 91. New York Botanical Garden Press, New York.

Chardon, C. E. 1947. La contribución del doctor Roberto E. Fries a los estudios botánicos del Nuevo Mundo. *Darwiniana* 7: 497-503.

Chase, M. W., Fay, M. F., Soltis, D. E., Soltis, P. S., Takahashi, K. T. & Savolainen, V. 2006. Simple phylogenetic tree searches easily "succeed" with large matrices of single genes. *Taxon* 55: 573-578.

Chatrou, L. W. 1997. Studies in Annonaceae XXVIII. Macromorphological variation of recent invaders in northern Central America: the case of *Malmea* (Annonaceae). *Amer. J. Bot.* 84: 861-869.

Chatrou, L. W., Rainer, H. & Maas, P. J. M. 2004. Annonaceae. Pp. 18-20 in: Smith, N., Mori, S. A., Henderson, A., Stevenson, D. W. & Heald, S. V., (Eds.), *Flowering Plants of the Neotropics*, Princeton University Press, Princeton, New Jersey, U.S.A.

Check, E. 2006. Treasure island: pinning down a model ecosystem. *Nature* 439: 378-379.

Chesters, K. I. M. 1955. Some plant remains from the Upper Cretaceous and Tertiary of West Africa. *Ann. Mag. Nat. Hist.* 12: 489-504.

Cieslak, T., Polepalli, J. S., White, A., Müller, K., Borsch, T., Barthlott, W., Steiger, J., Marchant, A. & Legendre, L. 2005. Phylogenetic analysis of *Pinguicula* (Lentibulariaceae): Chloroplast DNA sequences and morphology support several geographically distinct radiations. *Amer. J. Bot.* 92: 1723-1736.

Classen-Bockhoff, R., Speck, T., Tweraser, E., Wester, P., Thimm, S. & Reith, M. 2004. The staminal lever mechanism in *Salvia* L. (Lamiaceae): A key innovation for adaptive radiation? *Org. Divers. Evol.* 4: 189-205.

Coates, A. G. & Obando, J. A. 1996. The geological evolution of the Central American Isthmus. Pp. 21-56 in: Jackson, J. B. C., Budd, A. F. & Coates, A. G., (Eds.), *Evolution and environment in tropical America*, The University of Chicago Press, Chicago.

Colinvaux, P. 1996. Quaternary environmental history and forest diversity in the Neotropics. Pp. 359-405 in: Jackson, J. B. C., Budd, A. F. & Coates, A. G., (Eds.), *Evolution and environment in tropical America*, The University of Chicago Press, Chicago & London.

Colless, D. H. 1982. Review of phylogenetics: the theory and practice of phylogenetic systematics, by E.O. Wiley. *Syst. Zool.* 31: 100-104.

Couvreur, T. L. P., Gereau, R. E., Wieringa, J. J. & Richardson, J. E. in press. Description of four new species of *Monodora* and *Isolona* (Annonaceae) from Tanzania and an overview of Tanzanian Annonaceae diversity. *Adansonia*.

Cracraft, J. 1985. Biological diversity and it's causes. *Ann. Missouri Bot. Gard.* 72: 794-822.

Crawford, D. J. & Mort, M. E. 2004. Single-locus molecular markers for inferring relationships at lower taxonomic levels: observations and comments. *Taxon* 53: 631-635.

Cronn, R. C., Small, R. L., Haselkorn, T. & Wendel, J. F. 2002. Rapid diversification of the cotton genus (Gossypium: Malvaceae) revealed by analysis of sixteen nuclear and chloroplast genes. *Amer. J. Bot.* 89: 707-725.

Cronquist, A. 1978. Once again, what is a species? Pp. 3-20 in: Knutson, L. V., (Ed.), *Biosystematics in agriculture*, Allenheld Osmun, Montclair, New Jersey.

Csank, C., Taylor, F. M. & Martindale, D. W. 1990. Nuclear pre-mRNA introns: analysis and comparison of intron sequences from *Tetrahymena thermophila* and other eukaryotes. *Nucl. Acids Res.* 18: 5133-5141.

Cuénoud, P., Savolainen, V., Chatrou, L. W., Powell, M., Grayer, R. J. & Chase, M. W. 2002. Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid *rbcL*, *atpB,* and *matK* DNA sequences. *Amer. J. Bot.* 89: 132-144.

Cummings, M. P., Handley, S. A., Myers, D. S., Reed, D. L., Rokas, A. & Winka, K. 2003. Comparing Bootstrap and Posterior Probability Values in the Four-Taxon Case. *Syst. Biol.* 52: 477-487.

Dalton, R. 2003. Natural history collections in crisis as funding is slashed. *Nature* 423: 575.

Dannenfeldt, K. H. 1968. *Leonhard Rauwolf, sixteenth-century physician, botanist, and traveler*. Harvard University Press, Cambridge, Massachusetts, USA.

Davies, T. J., Barraclough, T. G., Chase, M. W., Soltis, P. S., Soltis, D. E. & Savolainen, V. 2004. Darwin's abominable mystery: Insights from a supertree of the angiosperms. *Proc. Natl. Acad. Sci. USA* 101: 1904-1909.

Davis, C. C., Bell, C. D., Fritsch, P. W. & Mathews, S. 2002. Phylogeny of Acridocarpus-Brachylophon (Malphigiaceae): Implications for Tertiary tropical floras and Afroasian biogeography. *Evolution* 56: 2395-2405.

Deroin, T. 1997. Confirmation and origin of the paracarpy in Annonaceae, with comments on some methodological aspects. *Candollea* 52: 45-58.

Derome, N., Métayer, K., Montchamp-Moreau, C. & Veuille, M. 2004. Signature of selective sweep associated with the evolution of sex-ratio drive in *Drosophila simulans*. *Genetics* 166: 1357-1366.

Després, L., Gielly, L., Redoutet, B. & Taberlet, P. 2003. Using AFLP to resolve phylogenetic relationships in a morphologically diversified plant species complex when nuclear and chloroplast sequences fail to reveal variability. *Mol. Phyl. Evol.* 27: 185-196.

Dias, P., Assis, L. C. S. & Udulutsch, R. G. 2005. Monophyly vs. paraphyly in plant systematics. *Taxon* 54: 1039-1040.

Dice, L. R. 1945. Measures of the amount of ecological association between species. *Ecology* 26: 297-302.

Diels, L. 1905. In: Pilger, R. - Beiträge zur Flora des Hylaea nach den Sammlungen von E. Ule. *Verh. Bot. Vereins Prov. Brandenburg* 47: 125-136; pl. 1.

Diels, L. 1906. In: Urban, I. - Plantae novae andinae imprimis Weberbauerianae. I. 9. Annonaceae andinae. *Bot. Jahrb. Syst.* 37: 408-410.

Diels, L. 1924a. In: Mildbread, J. - Plantae Tessmannianae peruvianae 1. *Notizbl. Bot. Gart. Berlin-Dahlem* 9: 137-141.

Diels, L. 1924b. Vermischte Diagnosen I. *Notizbl. Bot. Gart. Berlin-Dahlem* 9: 51-52.

Diels, L. 1927. In: Mildbread, J. - Plantae Tessmannianae peruvianae 6. *Notizbl. Bot. Gart. Berlin-Dahlem* 10: 76-77.

Diels, L. 1931. Annonaceae novae. *Notizbl. Bot. Gart. Berlin-Dahlem* 11: 73-86.

Diller, K. C., Gilbert, W. A. & Kocher, T. D. 2002. Selective sweeps in the human genome: a starting point for identifying genetic differences between modern humans and chimpanzees. *Mol. Biol. Evol.* 19: 2342-2345.

Douady, C. J., Delsuc, F., Boucher, Y., Ford Doolittle, W. & Douzery, E. J. P. 2003. Comparison of Bayesian and Maximum Likelihood bootstrap measures of phylogenetic reliability. *Mol. Biol. Evol.* 20: 248-254.

Doyle, J. J. & Doyle, J. L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phyt. Bull.* 19: 11-15.

Doyle, J. A. & Le Thomas, A. 1996. Phylogenetic analysis and character evolution in Annonaceae. *Adansonia* 18: 279-334.

Doyle, J. A. & Le Thomas, A. 1997a. Significance of palynology for phylogeny of Annonaceae: experiments with removal of pollen characters. *Pl. Syst. Evol.* 206: 133-159.

Doyle, J. A. & Le Thomas, A. 1997b. Phylogeny and geographic history of Annonaceae. *Géog. Phys. Quart.* 51: 353-361.

Doyle, J. A., Bygrave, P. & Le Thomas, A. 2000. Implications of molecular data for pollen evolution in Annonaceae. Pp. 259-284 in: Harley, M. M., Morton, C. M. & Blackmore, S., (Eds.), *Pollen and spores: morphology and biology*, Royal Botanic Garden Kew, UK.

Drábková, L., Kirschner, J. & Vlcek, C. 2002. Comparison of seven DNA extraction and amplification protocols in historical herbarium specimens of Juncaceae. *Plant. Mol. Biol. Rep.* 20: 161-175.

Dunal, M. F. 1817. *Monographie de la famille des Annonacées.* Treuttel & Würtz, Paris.

Eglinton, G., Logan, G. A., Ambler, R. P., Boon, J. J. & Perizonius, W. R. K. 1991. Molecular preservation [and discussion]. *Phil. Trans. R. Soc. Lond. B* 333: 315-328.

Ellis, J. 2002. Why impact factors don't work for taxonomy. *Nature* 415: 957.

Emshwiller, E. & Doyle, J. J. 2003. Chloroplast-expressed Glutamine Synthetase (ncpGS): potential utility for phylogenetic studies with an example from *Oxalis* (Oxalidaceae). *Mol. Phyl. Evol.* 12: 310-319.

Endress, P. K. 1982. Syncarpy and alternative modes of escaping disadvantages of apocarpy in primitive angiosperms. *Taxon* 31: 48-52.

Endress, P. K. 2001. Origins of flower morphology. *J. Exper. Zool.* 291: 105-115.

Erwin, D. H. 2006. Dates and rates: temporal resolution in the deep time stratigraphic record. *Annu. Rev. Earth Planet. Sci.* 34: 569-590.

Faith, D. P. & Cranston, P. S. 1991. Could a cladogram this sort have arisen by chance alone?: on permutation tests for cladistic structure. *Cladistics* 7: 1-28.

Faith, D. P. & Trueman, W. H. 2001. Towards an inclusive philosophy for phylogenetic inference. *Syst. Biol.* 50: 331-350.

Faith, D. P. 2004. From species to supertrees: Popperian corroboration and some current controversies in systematics. *Austral. Syst. Bot.* 17: 1-16.

Falco, C. M. 2006. Biodiversity data are out of local taxonomists reach. *Nature* 439: 392.

Farris, J. S. 1970. Methods for computing Wagner trees. *Syst. Zool.* 19: 83-92.

Farris, J. S., Kluge, A. G. & Eckardt, M. J. 1970. A numerical approach to phylogenetic systematics. *Syst. Zool.* 19: 172-189.

Farris, J. S., Källersjö, M., Kluge, A. G. & Bult, C. 1995. Testing significance of incongruence. *Cladistics* 10: 315-319.

Fay, M. F., Swensen, S. M. & Chase, M. W. 1997. Taxonomic affinities of *Medusagyne oppositifolia* (Medusagynaceae). *Kew Bull.* 52: 111-120.

Fay, M. F., Bayer, C., Alverson, S., de Bruijn, A. Y. & Chase, M. W. 1998. Plastid *rbcL* sequence data indicate a close affinity between *Diegodendron* and *Bixa*. *Taxon* 47: 43-50.

Felsenstein, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. *Syst. Zool.* 27: 401-410.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783-791.

Felsenstein, J. 1988. Phylogenies from molecular sequences: inference and reliability. *Annu. Rev. Genet.* 22: 521-565.

Felsenstein, J. 2004. *Inferring phylogenies.* Sinauer Associates, Inc., Sunderland MA.

Fine, P. V. A., Daly, D. C., Munoz, G. V., Mesones, I. & Cameron, K. M. 2005. The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western amazon. *Evolution* 59: 1464-1478.

Fitch, W. M. 1971. Toward defining the course of evolution: minimum change for a specified tree topology. *Syst. Zool.* 20: 406-416.

Foran, D. R. 2006. Relative degradation of nuclear and mitochondrial DNA: An experimental approach. *J. Forensic Sci.* 51: 766-770.**Fries, R. E.** 1930. Revision der Arten einiger Annonaceen-Gattungen I. *Acta Horti Berg.* 10: 1-128.

Fries, R. E. 1934. Revision der Arten einiger Anonaceen-Gattungen III. *Acta Horti Berg.* 12: 1-220.

Fries, R. E. 1938. Annonaceae in Macbride, J.F. - Flora of Peru. *Field Mus. Nat. Hist., Bot ser.* 13 (2): 700-766.

Fries, R. E. 1939. Revision der Arten einiger Annonaceen-Gattungen V. *Acta Horti Berg.* 12: 289-577.

Fries, R. E. 1943. Einige Gesichtspunkte zur systematischen Gruppierung der amerikanischen Annonaceen-Gattungen. *Ark. Bot.* 30A: 1-31.

Fries, R. E. 1947. Die Annonaceen der vierten Regnellschen Expedition. *Ark. Bot.* 33A: 1-20.

Fries, R. E. 1948a. Contributions to the flora of tropical America XLVII. Annonaceae new to British Guiana. *Kew Bull.* 1948: 229-235.

Fries, R. E. 1948b. New or noteworthy Annonaceae from tropical America. *Kongl. Svenska Vetenskapsakad. Handl., ser 3* 24: 3-19.

Fries, R. E. 1950a. Contributions to the knowledge of the Annonaceae in northern South America. *Ark. Bot.* n.s., 1: 329-331.

Fries, R. E. 1950b. Three new species of Annonaceae from Northern South America. *Ark. Bot.* n.s., 1: 445-451.**Fries, R. E.** 1952. Contributions to the flora of tropical America LIV. New trees and shrubs from British Guiana. *Kew Bull.* 1952: 255-257.

Fries, R. E. 1955a. Verstreute Beobachtungen hinsichtlich der Familie Annonaceae. *Ark. Bot.* n.s., 3: 35-42.

Fries, R. E. 1955b. Some new contributions to the knowledge of the Annonaceae in Colombia and Mexico. *Ark. Bot.* n.s., 3: 433-437.

Fries, R. E. 1957a. New species of Annonaceae from the Upper Amazon Basin. *Ark. Bot.* n.s., 3: 599-606.

Fries, R. E. 1957b. New species and new records of plants in Guiana. *Brittonia* 8: 231-245.

Fries, R. E. 1959a. Die Annonaceen der sechsten Regnellschen Expedition. *Ark. Bot.* n.s., 4: 23-27.

Fries, R. E. 1959b. Annonaceae. Pp. 1-171 in: Engler, A. & Prantl, K., (Eds.), *Die Natürlichen Pflanzenfamilien, ed. 2.*, vol. 17a II. Duncker & Humblot, Berlin.

Frodin, D. G. 2004. History and concepts of big plant genera. *Taxon* 53: 753-776.

Funk, V. A. 2003. The importace of herbaria. *Pl. Sci. Bull.* 49: 94-95.

Fusco, G. & Cronck, Q. C. B. 1995. A new method for evaluating the shape of large phylogenies. *J. Theor. Biol.* 175: 235-243.

Gatesy, J., O'Grady, P. & Baker, R. H. 1999. Corroboration among Data Sets in Simultaneous Analysis: Hidden Support for Phylogenetic Relationships among Higher Level Artiodactyl Taxa. *Cladistics* 15: 271-313.

Gentry, A. H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Ann. Missouri Bot. Gard.* 69: 557-593.

Gittenberger, E. 1991. What about non-adaptive radiation? *Biol. J. Linn. Soc.* 43: 263-272.

Gittenberger, E. 2004. Radiation and adaptation, evolutionary biology and semantics. *Org. Divers. Evol.* 4: 135-136.

Givnish, T. J. & Systma, K. J. 1997. *Molecular evolution and adaptive radiation*. Cambridge University Press, Cambridge.

Godfray, H. C. J. 2002. Challenges for taxonomy. *Nature* 417: 17-18.

Goldstein, D. B. & Pollock, D. D. 1997. Launching microsatellites: a review of mutation processes and methods of phylogenetic inference. *J. Hered.* 88: 335-342.

Gompert, Z., Nice, C. C., Fordyce, J. A., Forister, M. L. & Shapiro, A. M. 2006. Identifying units for conservation using molecular systematics: the cautionary tale of the Karner blue butterfly. *Molec. Ecol.* 15: 1759-1768.

Goodall, G. J. & Filipowicz, W. 1989. The AU-rich sequences present in the introns of plant nuclear pre-mRNAs are required for splicing. *Cell* 58: 473-483.

Gottsberger, G. 1999. Pollination and evolution in Neotropical Annonaceae. *Plant Sp. Biol.* 14: 143-152.

Grant, P. R. & Grant, B. R. 1996. Speciation and hybridization in island birds. *Phil. Trans. R. Soc. Lond. B* 351: 765-772.

Graybeal, A. 1998. Is it better to add taxa or characters to a difficult phylogenetic problem? *Syst. Biol.* 47: 9-17.

Griffiths, C. S. 1997. Correlation of functional domains and rates of nucleotide substitution in *Cytochrome b. Mol. Phyl. Evol.* 7: 352-365.

Gropp, R. E. 2003. Are university natural science collections going extinct? . *Bioscience* 53: 550.

Grote, D., Olmos, A., Kofoet, A., Tuset, J. J., Bertolini, E. & Cambra, M. 2002. Specific and sensitive detection of *Phytophthora nicotianae* by simple and nested-PCR. *Eur. J. Plant. Pathol.* 108: 197-207.**Halanych, K.** 2004. The new view of animal phylogeny. *Annu. Rev. Ecol. Syst.* 35: 229-256.

Hamilton, M. B. 1999. Four primer pairs for the amplification of chloroplast intergenic regions with intraspecific variation. *Molec. Ecol.* 8: 521-523.

Hawksworth, D. L. & Rossman, A. Y. 1997. Where are all the undescribed Fungi? *Phytopathology* 87: 887-891.

Heads, M. 2005. Dating nodes on molecular phylogenies: a critique of molecular biogeography. *Cladistics* 21: 62-78.

Heard, S. B. 1992. Patterns in tree balance among cladistic, phenetic, and randomly generated phylogenetic trees. *Evolution* 46: 1818-1826.

Heard, S. B. & Mooers, A. O. 1996. Imperfect information and the balance of cladograms and phenograms. *Syst. Biol.* 45: 115-118.

Hebert, P. D. N. & Gregory, R. T. 2005. The promise of DNA barcoding for taxonomy. *Syst. Biol.* 54: 852-859.

Helfenbein, K. G. & DeSalle, R. 2005. Falsifications and corroborations: Karl Popper's influence on systematics. *Mol. Phyl. Evol.* 35: 271.

Hennig, W. 1950. *Grundzüge einer Theorie der Phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin.

Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana.

Heusden, E. C. H. van 1992. Flowers of Annonaceae: morphology, classification, and evolution. *Blumea* Supplement 7: 1-218.

Hey, J. 2001. The mind of the species problem. *Trends Ecol. Evol.* 16: 326-329.

Hillis, D. M. 1996. Inferring complex phylogenies. *Nature* 383: 130-131.

Hofreiter, M., Poinar, H., Spaulding, W. G., Bauer, K., Martin, P. S., Possner, G. & Pääbo, S. 2000. A molecular analysis of ground sloth diet through the last glaciation. *Molec. Ecol.* 9: 1975-1984.

Holder, M. & Lewis, P. O. 2003. Phylogeny estimation: traditional and Bayesian approaches. *Nat. Rev. Gen.* 4: 275-284.

Hörandl, E. 2006. Paraphyletic versus monophyletic taxa—evolutionary versus cladistic classifications. *Taxon* 55: 564-570.

Huelsenbeck, J. P. & Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Version 3.1.1. *Bioinf.* 17: 754-755.

Hugenholtz, P. 2002. Exploring prokaryotic diversity in the genomic era. *Genome Biology* 3: reviews0003.1–0003.8.

Hull, D. L. 1976. Are species really individuals? *Syst. Zool.* 25: 174-191.

Hull, D. L. 1997. The ideal species concept - and why can't we get it. Pp. 357-380 in: Claridge, M. F., Dawah, H. A. & Wilson, M. R., (Eds.), *Species: the units of biodiversity*, Chapman & Hall, London.

Hunter, J. P. 1998. Key-innovations and the ecology of macroevolution. *Trends Ecol. Evol.* 13: 31-36.

Hilu, K. W., Borsch, T., Müller, K., Soltis, D. E., Soltis, P. S., Savolainen, V., Chase, M. W., Powell, M. P., Alice, L. A., Evans, R., Sauquet, H., Neinhuis, C., Slotta, T. A. B., Rohwer, J. G., Campbell, C. S. & Chatrou, L. W. 2003. Angiosperm phylogeny based on *matK* sequence information. *Amer. J. Bot.* 90: 1758-1776.

Hoot, S. B., Culham, A. & Crane, P. R. 1995. The utility of *atpB* gene sequences in resolving pylogenetic relationships: comparison with *rbcL* and 18S ribosomal DNA sequences in the Lardizabalaceae. *Ann. Missouri Bot. Gard.* 82: 194-207.

Hutchinson, J. 1923. Contributions towards a phylogenetic classification of flowering plants. II. The genera of Annonaceae. *Bull. Misc. Inform.* 1923: 241-261.

Hutchinson, J. 1964. Annonaceae. Pp. 71-108 in, *The genera of flowering plants. Dicotyledones 1*, Clarendon Press, Oxford.

IAWA Committee, 1989. IAWA List of Microscopic Features for Hardwood Identification. *IAWA Bull.* 10: 219-332.

Isaac, N. J. B., Agapow, P. & Harvey, P. H. 2003. Phylogenetically nested comparisons for testing correlates of species richness: a simulation study of continuous variables. *Evolution* 57: 18-26.

Iturralde-Vinent, M. A. & MacPhee, R. D. E. 1999. Palaeogeography of the Caribbean region: implications for Cenozoic biogeography. *Bull. Amer. Mus. Nat. Hist.* 238: 1-95.

Jackson, S., Rounsley, S. & Purugganan, M. 2006. Comparative sequencing of plant genoms: choices to make. *The Plant Cell* 18: 1100-1104.

Jankowiak, K., Buczkowska, K. & Szweykowska-Kulinska, Z. 2005. Successful extraction of DNA from 100-year-old herbarium specimens of the liverwort *Bazzania trilobata*. *Taxon* 54: 335-336.

James, T. Y., Kauff, F., Schoch, C. L. & al. 2006. Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature* 443: 818-822.

Jaynes, E. T. 1985. Bayesian methods: general background. Pp. 1-12 in: Justice, J. H., (Ed.), *Maximum entropy and Bayesian methods in applied statistics*, Cambridge University Press.

Johnson, D. M. 2003. Phylogenetic significance of spiral and distichous architecture in the Annonaceae. *Syst. Bot.* 28: 503-511.

Jonsell, B., Broberg, G., Eriksson, G. & Nordenstam, B. 1991. *Bergianska botanister.* Atlantis, Stockholm, Sweden.

Källersjö, M., Farris, J. S., Chase, M. W., Bremer, B., Fay, M. F., Humphries, C. J., Petersen, G., Seberg, O. & Bremer, K. 1998. Simultaneous parsimony jackknife analysis of 2538 *rbcL* DNA sequences reveals support for major clades of green plants, land plants, seed plants and flowering plants. *Pl. Syst. Evol.* 213: 259-287.

Kim, K.-J. & Jansen, R. K. 1995. *ndhF* sequence evolution and the major clades in the sunflower family. *Proc. Natl. Acad. Sci. USA* 92: 10379-10383.

Kim, S., Park, C.-W., Kim, Y.-D. & Suh, Y. 2001. Phylogenetic relationships in family Magnoliaceae inferred from *ndhF* sequences. *Amer. J. Bot.* 88: 717-728.

Kimura, M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J. Mol. Evol.* 16: 111-120.

Kirkpatrick, M. & Slatkin, M. 1993. Searching for evolutionary patterns in the shape of a phylogenetic tree. *Evolution* 47: 1171-1181.

Kluge, A. G. 1998. Total evidence or taxonomic congruence: cladistics or consensus classification. *Cladistics* 14: 151-158.

Kluge, A. G. 2002. Distinguishing "or" from "and", and the case for historical identification. *Cladistics* 18: 585-593.

Knoop, V. 2004. The mitochondrial DNA of land plants: peculiarities in phylogenetic perspective. *Cur. Genet.* 46: 123-139.

Koek-Noorman, J., Westra, L. Y. T. & Maas, P. J. M. 1990. Studies in Annonaceae. XIII. The role of morphological characters in subsequent classifications of Annonaceae: a comparative survey. *Taxon* 39: 16-32.

Koek-Noorman, J., Setten, A. K. v. & Zuilen, C. M. v. 1997. Studies in Annonaceae XXVI. Flower and fruit morphology in Annonaceae. Their contribution to patterns in cluster analysis. *Bot. Jahrb. Syst.* 119: 213-230.

Koopman, W. J. M., Zevenbergen, M. J. & van den Berg, R. G. 2001. Species relationships in *Lactuca* s.l. (Lactuceae, Asteraceae) inferred from AFLP fingerprints. *Amer. J. Bot.* 88: 1881-1887.

Koopman, W. J. M. 2005. Phylogenetic signal in AFLP data sets. *Syst. Biol.* 54: 197-217.

Leopold, E. B. & MacGinitie, H. D. 1972. Development and affinities of tertiary floras in the Rocky Mountains. Pp. 147-200 in: Graham, A., (Ed.), *Floristics and paleofloristics of Asia and Eastern North America*, Elsevier Publishing Company, Amsterdam.

Leebens-Mack, J., Vision, T., Brenner, E. & al. 2006. Taking the first steps towards a standard for reporting on phylogenies: minimum information about a phylogenetic analysis (MIAPA). *OMICS* 10: 231-237.

Levin, R. A., Wagner, W. L., Hoch, P. C., Nepokroeff, M., Pires, J. C., Zimmer, E. A. & Sytsma, K. J. 2003. Family-level relationships of Onagraceae based on chloroplast *rbcL* and *ndhF* data. *Amer. J. Bot.* 90: 107-115.

Lewis, P. O. 2000. EEB 372 Lectures, Class 14: Bayesian approach to phylogenetics. in.

Liolios, K., Tavernarakis, N., Hugenholtz, P. & al. 2006. The Genomes On Line Database (GOLD) v.2: a monitor of genome projects worldwide. *Nucl. Acids Res.* 34: D332-D334.

Losos, J. B. & Miles, D. B. 2002. Testing the hypothesis that a clade has adaptively radiated: Iguanid lizard clades as a case study. *Am. Nat.* 160: 147-157.

Maas, P. J. M., van Heusden, E. C. H., Koek-Noorman, J., van Setten, A. K. & Westra, L. Y. T. 1988. Studies in Annonaceae. IX. New species from the Neotropics and miscellaneous notes. *Proc. Kon. Ned. Akad. Wetensch. Ser. C* 91: 243-282.

Maddison, W. 1989. Reconstructing character evolution on polytomous cladograms. *Cladistics* 5: 365-377.

Maddison, D. R. & Maddison, W. P., 2000. MacClade: Analysis of Phylogeny and Character Evolution. Version 4.0. Sinauer Associates Inc., Sunderland, Massachusetts, U.S.A.

Maddison, W. P. 2006. Confounding asymmetries in evolutionary diversification and character change. *Evolution* 60: 1743–1746.

Madriñán, S. 2004. Lauraceae (Avocado Family). Pp. 204-206 in: Smith, N., Mori, S. A., Henderson, A., Stevenson, D. W. & Heald, S. V., (Eds.), *Flowering plants of the Neotropics*, Princeton University Press, Princeton, New Jersey, U.S.A.

Magallon, S. & Sanderson, M. J. 2001. Absolute diversification rates in Angiosperm clades. *Evolution* 55: 1762-1780.

Maguire, B., Wurdack, J. J. & Collaborators 1957. The botany of the Guayana highland - part II. *Mem. New York Bot. Gard.* 9: 235-392.

Maguire, B., Wurdack, J. J. & Collaborators 1960. The botany of the Guayana highland - part IV. *Mem. New York Bot. Gard.* 10: 22-23.

Maia, J. G. S., Andrade, E. H. A., Carreira, L. M. M., Oliveira, J. & Araújo, J. S. 2005a. Essential oils of the Amazon *Guatteria* and *Guatteriopsis* species. *Flav. Frag. J.* 20: 478-480.

Maia, J. G. S., Andrade, E. H. A., da Silva, A. C. M., Oliveira, J., Carreira, L. M. M. & Araújo, J. S. 2005b. Leaf volatile oils from four Brazilian *Xylopia* species. *Flav. Frag. J.* 20: 474-477.

Margulies, M., Egholm, M., Altman, W. E. & al. 2005. Genome sequencing in microfabricated high-density picolitre reactors. *Nature* 437: 376-380.

Martin, A. P. & Palumbi, S. R. 1993. Body size, metabolic rate, generation time, and the molecular clock. *Proc. Natl. Acad. Sci. USA* 90: 4087-4091.

Martius, C. F. P. von 1841. Annonaceae in, *von Martius, C.F.Ph. - Flora brasiliensis*, vol. 13. Pp. 1-64; pl. 1-14. Frid. Fleischer in comm., Munchen, Leipzig.

May, R. M. 1988. How many species are there on earth? *Science* 241: 1441-1449.

Mayden, R. L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. Pp. 381-424 in: Claridge, M. F., Dawah, H. A. & Wilson, M. R., (Eds.), *Species: the units in biodiversity*, Chapman & Hall, London.

Mayr, E. & Bock, W. J. 2002. Classifications and other ordering systems. *J. Zool. Syst. Evol. Research* 40: 169-192.

McConway, K. J. & Sims, H. J. 2004. A likelihood-based method for testing for nonstochastic variation of diversification rates in phylogenies. *Evolution* 58: 12-23.

Meade, C. V. & Parnell, J. A. 1998. Revision of *Uvaria* L. in continental Southeast Asia: 1. Stamen and carpel structure. *Annonaceae Newsletter* 12: 47-55.

Metcalfe, C. R. & Chalk, L. 1987. *Anatomy of the Dicotyledons. sec.ed. vol. III. Magnoliales, Illiciales, and Laurales.* Clarendon Press, Oxford.

Metzker, M. L. 2005. Emerging technologies in DNA sequencing. *Genome Research* 15: 1767-1776.

Mols, J. B. 2004. *From Miliusa to Miliuseae to Miliusoid: identifying clades in Asian Annonaceae.* PhD thesis, Universiteit Leiden.

Mols, J. B., Gravendeel, B., Chatrou, L. W., Pirie, M. D., Bygrave, P. C., Chase, M. W. & Kessler, P. J. A. 2004. Identifying clades in Asian Annonaceae: monophyletic genera in the polyphyletic Miliuseae. *Amer. J. Bot.* 91: 590-600.

Mooers, A. O., Page, R. D. M., Purvis, A. & Harvey, P. H. 1995. Phylogenetic noise leads to unbalanced cladistic tree reconstruction. *Syst. Biol.* 44: 332-342.

Mooers, A. O. & Heard, S. B. 1997. Inferring evolutionary process from phylogenetic tree shape. *Q. Rev. Biol.* 72: 31-54.

Moore, B. R., Chan, K. M. A. & Donoghue, M. J. 2004. Detecting diversification rate variation in supertrees. Pp. 487-533 in: Bininda-Edmonds, O. R. P., (Ed.), *Phylogenetic supertrees: combining information to reveal the tree of life*, Kluwer Academic Publishers, Dordrecht, The Netherlands.

Morawetz, W. 1984. Systematische un ökologische Bedeutung des Riesenstrauchwuchses von *Guatteria obovata* (Annonaceae) in den Überschwemmungswäldern Amazoniens. *Anz. Öst. Ak. Wiss.* 5: 59-62.

Morawetz, W. & Maas, P. J. M. 1984. Notes on the systematics of the Amazonian genus *Guatteriella* (Annonaceae). *Pl. Syst. Evol.* 148: 19-23.

Morawetz, W. & Waha, M. 1985. A new pollentype, C-banded and fluorochrome counterstained chromosomes, and evolution in *Guatteria* and related genera (Annonaceae). *Pl. Syst. Evol.* 150: 119-141.

Morrison, C. L., Ríos, R. & Duffy, J. E. 2004. Phylogenetic evidence for an ancient rapid radiation of Caribbean sponge-dwelling snapping shrimps (*Synalpheus*). *Mol. Phyl. Evol.* 30: 563-581.

Müller, K. F., Borsch, T. & Hilu, K. 2006. Phylogenetic utility of rapidly evolving DNA at high taxonomical levels: Contrasting *matK*, *trnT-F*, and *rbcL* in basal angiosperms. *Mol. Phyl. Evol.* 41: 99-117.

Murray, N. A. 1993. Revision of *Cymbopetalum* and *Porcelia* (Annonaceae). *Syst. Bot. Monogr.* 40: 1-121.

Nathan, R. 2006. Long-distance dispersal of plants. *Science* 313: 786-788.

Nei, M. & Li, W.-H. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proc. Natl. Acad. Sci. USA* 76: 5269-5273.

Nei, M. 1987. *Molecular Evolutionary Genetics.* Columbia University Press, New York.

Neuhaus, H. & Link, G. 1987. The chloroplast tRNA (UUU) gene from mustard (*Sinapsis alba*) contains a class II intron potentially coding for maturase-related polypeptide. *Cur. Genet.* 11: 251-257.

Nixon, K. C. & Carpenter, J. M. 1996. On simultaneous analysis. *Cladistics* 12: 221-241.

Nosil, P. & Crespi, B. J. 2006. Experimental evidence that predation promotes divergence in adaptive radiation. *Proc. Natl. Acad. Sci. USA* 103: 9090-9095.

Oliveira, A. A. & Mori, S. A. 1999. A central Amazonian terra firme forest. I. High tree species richness on poor soils. *Biodiv. Cons.* 8: 1219.

Olmstead, R. G., Michaels, H. J., Scott, K. M. & Palmer, J. D. 1992. Monophyly of the Asteridae and identification of major lineages inferred from DNA sequences of *rbc*L. *Ann. Missouri Bot. Gard.* 79: 249-265.

Olmstead, R. G. & Sweere, J. A. 1994. Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the Solanaceae. *Syst. Biol.* 43: 467-481.

Olmstead, R. G. & Palmer, J. D. 1994. Chloroplast DNA systematics: a review of methods and data analysis. *Amer. J. Bot.* 81: 1205-1224.

Olmstead, R. G. & Reeves, P. A. 1995. Evidence for the polyphyly of the Scrophulariaceae based on chloroplast *rbcL* and *ndhF* sequences. *Ann. Missouri Bot. Gard.* 82: 176-193.

Pääbo, S., Poinar, H., Serre, D., Jaenicke-Despées, V., Hebler, J., Rohland, N., Kuch, M., Krause, J., Vigilant, L. & Hofreiter, M. 2004. Genetic analyses from ancient DNA. *Annu. Rev. Genet.* 38: 645-679.

Page, T. J., Choy, S. C. & Hughes, J. M. 2005. The taxonomic feedback loop: symbiosis of morphology and molecules. *Biol. Lett.* 1: 139-142.

Pelser, P. B., Gravendeel, B. & van der Meijden, R. 2003. Phylogeny reconstruction in the gap between too little and too much divergence: the closest relatives of *Senecio jacobaea* (Asteraceae) according to DNA sequences and AFLP's. *Mol. Phyl. Evol.* 29: 613-628.

Pennington, R. T. & Dick, C. W. 2004. The role of immigrants in the assembly of the South American rainforest tree flora. *Phil. Trans. R. Soc. Lond. B* 359: 1611-1622.

Pennington, R. T., Lavin, M., Prado, D. E., Pendry, C. A., Pell, S. K. & Butterworth, C. A. 2004. Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Phil. Trans. R. Soc. Lond. B* 359: 515-538.

Pennington, T. D. 1981. Meliaceae. *Flora Neotropica* 28: 1-470.

Pennington, T. D. 1997. *The genus Inga. Botany*. Royal Botanic Gardens, Kew, London.

Phillimore, A. B., Freckleton, R. P., Orme, C. D. L. & Owens, I. P. F. 2006. Ecology predicts large-scale patterns of phylogenetic diversification in birds. *Am. Nat.* 168: 220-229.

Philippe, H. & Telford, M. J. 2006. Large-scale sequencing and the new animal phylogeny. *Trends Ecol. Evol.* 21: 614-620.

Pirie, M. D., Balcázar Vargas, M. P., Botermans, M., Bakker, F. T. & Chatrou, L. W. 2005a. Duplication of the cpDNA trnL (UAA)-trnF (GAA) region in Annonaceae and its application in phylogeny reconstruction. Pp. 65-85 in, *Cremastosperma (and other evolutionary digressions). Molecular phylogenetic, biogeographic, and taxonomic studies in Neotropical Annonaceae*, PhD-thesis, Utrecht University, Utrecht, The Netherlands.

Pirie, M. D., Chatrou, L. W., Erkens, R. H. J., Maas, J. W., Van der Niet, T., Mols, J. B. & Richardson, J. E. 2005b. Phylogeny reconstruction and molecular dating in four Neotropical genera of Annonaceae: the effect of taxon sampling in age estimations. Pp. 149-174 in: Bakker, F. T., Chatrou, L. W., Gravendeel, B. & Pelser, P. B., (Eds.), *Plant species-level systematics: new perspectives on pattern and process*, Regnum Vegetabile 143, A. R. G. Gantner Verlag, Liechtenstein.

Pirie, M. D., Chatrou, L. W., Mols, J. B., Erkens, R. H. J. & Oosterhof, J. 2006. 'Andean-centred' genera in the short-branch clade of Annonaceae: Testing biogeographic hypotheses using phylogeny reconstruction and molecular dating. *J. Biogeogr.* 33: 31-46.

Posada, D. & Crandall, K. A. 1998. Modeltest: testing the model of DNA substitution. *Bioinf.* 14: 817-818.

Posadas, P., Crisci, J. V. & Katinas, L. 2006. Historical biogeography: A review of its basic concepts and critical issues. *J. Arid Environ.* 66: 389-403.

Purvis, A. & Hector, A. 2000. Getting the measure of biodiversity. *Nature* 405: 212-219.

Queiroz, K. de 1988. Systematics and the Darwinian revolution. *Philos. Sci.* 55: 238-259.

Queiroz, K. de & Donoghue, M. J. 1990. Phylogenetic systematics and species revisited. *Cladistics* 6: 83-90.

Queiroz, K. de & Poe, S. 2001. Philosophy and phylogenetic inference: a comparison of likelihood and parsimony methods in the context of Karl Popper's writings on corroboration. *Syst. Biol.* 50: 305-321.

Queiroz, K. de & Poe, S. 2003. Failed Refutations: Further Comments on Parsimony and Likelihood Methods and Their Relationship to Popper's Degree of Corroboration. *Syst. Biol.* 52: 352-367.

Raikow, R. J. 1988. The analysis of evolutionary success. *Syst. Zool.* 37: 76-79.

Ratnayake, R. M. C. S., Gunatilleke, I. A. U. N., Wijesundara, D. S. A. & Saunders, R. M. K. 2006. Reproductive biology of two sympatric species of *Polyalthia* (Annonaceae) in Sri Lanka. I. Pollination by curculionid beetles. *Int. J. Plant Sci.* 167: 483-493.

Raven, P. H. & Axelrod, D. L. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539-673.

Renner, S. S. & Meyer, K. 2001. Melastomeae come full circle: biogeographic reconstruction and molecular clock dating. *Evolution* 55: 1315-1324.

Renner, S. S. 2004. Variation in diversity among Laurales, Early Cretaseous to Present. *Biol. Skr.* 55: 441-458.

Richardson, J. E., Pennington, R. T., Pennington, T. D. & Hollingsworth, P. M. 2001a. Rapid diversification of a species-rich genus of Neotropical rainforest trees. *Science* 293: 2242-2245.

Richardson, J. E., Weitz, F. M., Fay, M. F., Cronk, Q. C. B., Linder, H. P., Reeves, G. & Chase, M. W. 2001b. Phylogenetic analysis of *Phylica* L. (Rhamnaceae) with an emphasis on island species: evidence from the plastid trnL-F and nuclear transcribed spacer (ribosomal) DNA sequences. *Taxon* 50: 405-427.

Richardson, J. E., Chatrou, L. W., Mols, J. B., Erkens, R. H. J. & Pirie, M. D. 2004. Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae. *Phil. Trans. R. Soc. Lond. B* 359: 1495-1508.

Ricklefs, R. E. 2003. Global diversification rates of passerine birds. *Proc. R. Soc. Lond. B Bio.* 270: 2285-2291.

Ridley, M. 1989. The cladistic solution to the species problem. *Biol. Philos.* 4: 1-16.

Rogers, S. O. & Bendich, A. J. 1985. Extraction of DNA from milligram amounts of fresh, herbarium and mummified plant tissues. *Pl. Mol. Biol.* 5: 69-76.

Rohlf, F. J. 2005. *NTSYS-PC: numerical taxonomy and multivariate analysis system, version 2.20d.* Applied Biostatistics Inc., Setauket, New York, USA.

Rohland, N., Siedel, H. & Hofreiter, M. 2004. Nondestructive DNA extracion method for mitochondrial DNA analyses of museum specimens. *BioTechniques* 36: 814-821.

Rohwer, J. G. 2005. Flora Neotropica Monograph 91 & 92, book review. *Syst. Biol.* 54: 860.

Ronquist, F. & Huelsenbeck, J. P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinf.* 19: 1572-1574.

Rosenzweig, M. L. 1978. Geographical speciation: on range size and the probability of isolate formation. Pp. 172-194 in: Wolkind, D., (Ed.), *Proceedings of the Washington State University Conference on Biomathemathics and Biostatistics*, Pullman.

Rüber, L., Van Tassel, J. L. & Zardoya, R. 2003. Rapid speciation and ecological divergence in the American seven-spined gobies (Gobiidae, Gobiosomatini) inferred from a molecular phylogeny. *Evolution* 57: 1584-1598.

Ruiz Lopez, H. & Pavón, J. A. 1794. *Florae peruvianae, et chilensis prodromus*. Imprenta de Sancha, Madrid.

Ruiz Lopez, H. & Pavón, J. A. 1798. *Systema vegetabilium florae peruvianae et chilensis.* Gabrielis de Sancha, Madrid.

Saint-Hilaire, A. F. C. P. de 1824/25. *Flora Brasiliae meridionalis*. Paris, apud A. Belin.

Saitou, N. & Nei, M. 1987. The neighbour-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* 4: 406-425.

Sánchez S., D. 1986. *Revisión de la sección Chasmantha del genero Guatteria (Annonaceae)*. PhD thesis, Universidad Nacional de Colombia Bogotá, Colombia.

Sanders, R. W. & Judd, W. S. 2000. Incorporating phylogenetic results into floristic treatments. *SIDA, Bot. Misc.* 18: 97-112.

Sanderson, M. J. & Donoghue, M. J. 1994. Shifts in diversification rate with the origin of Angiosperms. *Science* 264: 1590-1593.

Sanderson, M. J. & Donoghue, M. J. 1996. Reconstructing shifts in diversification rates on phylogenetic trees. *Trends Ecol. Evol.* 11: 15-20.**Sanderson, M. J.** 1997. A nonparametric approach to estimating divergence times in the absence of rate constancy. *Mol. Biol. Evol.* 14: 1218-1231.

Sanderson, M. J. 1998. Reappraising adaptive radiation. *Amer. J. Bot.* 85: 1650-1655.

Sanderson, M. J. 2002. Estimating absolute rates of molecular evolution and divergence times: a penalised likelihood approach. *Mol. Biol. Evol.* 19: 101-109.

Sanderson, M. J. & Driskell, A. C. 2003. The challenge of reconstructing large phylogenetic trees. *Trends Plant Sci.* 8: 374-379.

Sanderson, M. J. 2004. r8s, version 1.7. Distributed by the author, Section of Evolution and Ecology, University of California, Davis, Davis, CA.

Sang, T. 2002. Utility of low-copy nuclear gene sequences in plant phylogenetics. *Crit. Rev. Biochem. Mol. Biol.* 37: 121-147.

Sauquet, H., Doyle, J. A., Scharaschkin, T., Borsch, T., Hilu, K., Chatrou, L. W. & Le Thomas, A. 2003. Phylogenetic analysis of Magnoliales and Myristicaceae based on multiple data sets: implications for character evolution. *Bot. J. Linn. Soc.* 142: 125-186.

Savolainen, V., Cuénoud, P., Spichiger, R., Martinez, M. D. P., Crèvecoeur, M. & Manen, J. F. 1995. The use of herbarium specimens in DNA phylogenetics: evaluation and improvement. *Pl. Syst. Evol.* 197: 87-98.

Savolainen, V., Heard, S. B., Powell, M. P., Davies, T. J. & Mooers, A. O. 2002. Is cladogenesis heritable? *Syst. Biol.* 51: 835-843.

Scharf, U., Maas, P. J. M. & Morawetz, W. 2005. Five new species of *Guatteria* (Annonaceae) from the Pakaraima mountains. *Blumea* 50: 563-573.

Scharf, U., Maas, P. J. M. & Morawetz, W. 2006a. *Guatteria richardii* (Annonaceae) rediscovered along with two new species from French Guiana. *Blumea* 51: 541-552.

Scharf, U., Maas, P. J. M. & Morawetz, W. 2006b. Five new species of *Guatteria* (Annonaceae) from French Guiana, Guyana and Suriname. *Blumea* 51: 117-130.

Scharaschkin, T. & Doyle, J. A. 2005. Phylogeny and historical biogeography of Anaxagorea (Annonaceae) using morphology and non-coding chloroplast sequence data. *Syst. Bot.* 30: 712-735.

Schatz, G. E. 1987. *Systematic and ecological studies in Central American Annonaceae*. PhD-thesis. University of Wisconsin, Madison.

Schlechtendahl, D. F. L. von 1834. De Annonaceis Brasiliensibus Herbarii Regii Berolinensis. *Linnaea* 9: 315-331.

Schluter, D. 2000. *The ecology of adaptive radiation*. Oxford University Press, Oxford.

Schneeweiss, G. M., Schönswetter, P., Kelso, S. & Niklfeld, H. 2004. Complex biogeographic patterns in *Androsace* (Primulaceae) and related genera: evidence from phylogenetic analyses of nuclear internal transcribed spacer and plastid *trnL-F* sequences. *Syst. Biol.* 53: 856-876.

Schneider, H., Russell, S. J., Cox, C. J., Bakker, F. T., Henderson, S., Rumsey, F., Barrett, J., Gibby, M. & Vogel, J. C. 2004. Chloroplast phylogeny of Asplenioid ferns based on *rbcL* and *trnL-F* spacer sequences (Polypodiidae, Aspleniaceae) and its implications for biogeography. *Syst. Bot.* 29: 260-274.

Scotland, R. W., Hughes, C., Bailey, D. & Wortley, A. 2003. The *Big Machine* and the much maligned taxonomist. *Syst. Biodiv.* 1: 139-143.

Setten, A. K. van & Koek-Noorman, J. 1986. Studies in Annonaceae. VI. A leafanatomical survey of genera of Annonaceae in the Neotropics. *Bot. Jahrb. Syst.* 108: 17-50.

Setten, A. K. van & Maas, P. J. M. 1990. Studies in Annonaceae. XIV. Index to generic names of Annonaceae. *Taxon* 39: 675-690.

Setten, A. K. van & Koek-Noorman, J. 1992. Studies in Annonaceae. XVII. Fruits and seeds of Annonaceae: morphology and its significance for classification. *Biblioth. Bot.* 142: 1-101.

Shao, K.-T. & Sokal, R. R. 1990. Tree balance. *Syst. Zool.* 39: 266-276.

Shaw, J., Lickey, E. B., Beck, J. T., Farmer, S. B., Liu, W., Miller, J., Siripun, K. C., Winder, C. T., Schilling, E. E. & Small, R. L. 2005. The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *Amer. J. Bot.* 92: 142-166.

Shi, X., Gu, H., Susko, E. & Field, C. 2005. The comparison of the confidence regions in phylogeny. *Mol. Biol. Evol.* 22: 2285-2296.

Simmons, M. P. & Ochoterena, H. 2000. Gaps as characters in sequence-based phylogenetic analysis. *Syst. Biol.* 49: 369-381.

Simmons, M. P., Pickett, K. M. & Miya, M. 2004. How Meaningful Are Bayesian Support Values? *Mol. Biol. Evol.* 21: 188-199.

Simmons, M. P., Zhang, L.-B., Webb, C. T., Reeves, A. & Miller, J. A. 2006. The relative performance of Bayesian and parsimony approaches when sampling characters evolving under homogeneous and heterogeneous sets of parameters. *Cladistics* 22: 171-185.

Simões, A. O., Endress, M. E., Van der Niet, T., Kinoshita, L. S. & Conti, E. 2004. Tribal and intergeneric relationships of Mesechiteae (Apocynoideae, Apocynaceae): evidence from three noncoding plastid DNA regions and morphology. *Amer. J. Bot.* 91: 1409-1418.

Simpson, B. B. 1975. Pleistocene changes in the flora of the high tropical Andes. *Paleobiology* 1: 273-294.

Simpson, D. R. 1982. New species from South America III. *Phytologia* 51: 305-308.

Skelton, P. W. 1993. Adaptive radiation: definition and diagnostic tests. Pp. 45-58 in: Lees, D. R. & Edwards, D., (Eds.), *Evolutionary patterns and processes*, The Linnean Society of London, London.

Slowinsky, J. B. & Guyer, C. 1989a. Testing the stochasticity of patterns of organismal diversity: an improved null model. *Am. Nat.* 134: 907-921.

Slowinsky, J. B. & Guyer, C. 1989b. Testing null models in questions of evolutionary success. *Syst. Zool.* 38: 189-191.

Slowinsky, J. B. 1990. Probabilities of *n*-trees under two models: demonstration that asymmetrical interior nodes are not improbable. *Syst. Zool.* 39: 89-94.

Slowinsky, J. B. & Guyer, C. 1993. Testing whether certain traits have caused amplified diversification: an improved method based on a model of random speciation and extinction. *Am. Nat.* 142: 1019-1024.**Smith, N., Mori, S. A., Henderson, A., Stevenson, D. W. & Heald, S. V.** 2004. *Flowering Plants of the Neotropics*. Princeton University Press, Princeton, New Jersey.

Smith, G. F., van Wijk, A. E., Johnson, L. M. & van Wijk, B.-E. 1996. Southern African plant systematics: needs, priorities and actions. *S. African J. Sci.* 92: 314-320.

Smith, G. F. 2006. Herbaria in the real world. *Taxon* 55: 571-572.

Smith, J. M. & Haigh, J. 1974. The hitch-hiking effect of a favourable gene. *Genet. Res.* 23: 23-35.

Sober, E. 1994. *From a biological point of view*. Cambridge University Press, Cambridge, England.

Soltis, D. E., Kuzoff, R. K., Conti, E., Gornall, R. & Ferguson, K. 1996. *matK* and *rbcL* gene sequence data indicate that *Saxifraga* (Saxifragaceae) is polyphyletic. *Amer. J. Bot.* 83: 371-382.

Soltis, D. E. & Soltis, P. S. 1998. Choosing an approach and an appropriate gene for phylogenetic analysis. Pp. 574 in: Soltis, D. E., Soltis, P. S. & Doyle, J. J., (Eds.), *Molecular systematics of plants II, DNA sequencing*, Kluwer Academic Publishers, Boston/Dordrecht/London.

Soltis, D. E., Soltis, P. S., Chase, M. W., Mort, M. E., Albach, D. C., Zanis, M., Savolainen, V., Hahn, W. H., Hoot, S. B., Fay, M. F., Axtell, M., Swensen, S. M., Prince, L. M., Kress, W. J., Nixon, K. C. & Farris, J. S. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Bot. J. Linn. Soc.* 133: 381-461.

Soltis, D. E., Albert, V. A., Savolainen, V., Hilu, K., Qui, Y.-L., Chase, M. W., Farris, J. S., Stefanovic, S., Rice, D. W., Palmer, J. D. & Soltis, P. S. 2004. Genome-scale data, angiosperm relationships, and 'ending incongruence': a cautionary tale in phylogenetics. *Trends Plant Sci.* 9: 477-483.

Steel, M. A. 1993. Confidence in evolutionary trees from biological sequence data. *Nature* 364: 440-442.

Steyermark, J. A. & Berry, P. E. 1995. *Heteropetalum* Benth. Pp. 452-453 in: Steyermark, J. A., Berry, P. E. & Holst, B. K., (Eds.), *Flora of the Venezuelan Guayana*, vol. 2. Timber Press, Inc., Portland, Oregon, U.S.A.

Sudhaus, W. 2004. Radiation within the framework of evolutionary ecology. *Org. Divers. Evol.* 4: 127-134.

Swofford, D. L., 2003. PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods). Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.

Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. 1991. Universal primers for amplification of the three non-coding regions of chloroplast DNA. *Pl. Mol. Biol.* 17: 1105-1109.

Takhtajan, A. L. 1986. *Floristic regions of the world*. University of California Press, Berkeley, California.

Templeton, A. R. 1981. Mechanisms of speciation—a population genetic approach. *Annu. Rev. Ecol. Syst.* 12: 23-48.

Triana, J. J. & Planchon, J. É. 1862. Prodromus florae novo-granatensis. *Ann. Sci. Nat. Bot.* sér. 4, 17: 25-40.

Templeton, A. R. 2001. Using phylogeographic analyses of gene trees to test species status and progress. *Molec. Ecol.* 10: 779-791.

Threadgold, J. & Brown, T. A. 2003. Degradation of DNA in artificially charred wheat seeds. *J. Archeol. Sci.* 30: 1067-1076.

Tsou, C.-H. & Johnson, D. M. 2003. Comparative development of aseptate and septate anthers of Annonaceae. *Amer. J. Bot.* 90: 832-848.

Tuskan, G. A., DiFazio, S., Jansson, S. & al. 2006. The Genome of Black Cottonwood, *Populus trichocarpa* (Torr. & Gray). *Science* 313: 1596-1604.

Unknown 1966. Robert Elias Fries (obituary). *Taxon* 15: 128.

Unknown 2001. Insights in processes of plant evolution. *Taxon* 50: 5-6.

Vamosi, S. M. & Vamosi, J. C. 2005. Endless tests: Guidelines for analysing non-nested sister-group comparisons. *Evol. Ecol. Res.* 7: 567-579.

Vavilov, N. I. 1935. *Principles and methods of plant breeding*. Institute of field and vegetable crops, University of Novi Sad, Yugoslavia.

Verheyen, S., Salzburger, W., Snoeks, J. & Meyer, A. 2003. Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. *Science* 300: 325-329.

Vermeij, G. J. 1973. Biological versatility and earth history. *Proc. Natl. Acad. Sci. USA* 70: 1936-1938.

Voronov, D. A., Panchin, Y. V. & Spiridonov, S. E. 1998. Nematode phylogeny and embryology. *Nature* 395: 28.

Vos, P., Hogers, R., Bleeker, M., Reijans, M., Lee, T. v. d., Hornes, M., Friters, A., Pot, J., Paleman, J., Kuiper, M. & Zabeau, M. 1995. AFLP: a new technique for DNA fingerprinting. *Nucl. Acids Res.* 23: 4407-4414.

Waha, M. 1987. Different origins of fragile exines within the Annonaceae. *Pl. Syst. Evol.* 158: 23-27.

Walker, J. M. 1971. Pollen morphology, phytogeography and phylogeny of the Annonaceae. *Contr. Gray Herb.* 202: 1-133.

Wang, A., Yang, M. & Liu, J. 2005. Molecular phylogeny, recent radiation and evolution of gross morphology of the rhubarb genus *Rheum* (Polygonaceae) inferred from chloroplast DNA *trnL-F* sequences. *Ann. Bot.* 96: 489-498.

Ward, B. B. 2002. How many species of prokaryotes are there? *Proc. Natl. Acad. Sci. USA* 99: 10234-10236.

Webber, A. C. 2002. Floral biology and pollination of some Neotropical Annonaceae. *Annonaceae Newsletter* 13: 18-21.

Westra, L.Y.T. & Koek-Noorman, J. In prep. Wood features of Annonaceae. In: Chatrou L.W. & al. (eds.). Natural History of the Annonaceae. A.R.G. Gantner Verlag, Ruggell, Lichtenstein (Renum Vegetabile).

Wheeler, E. A. & al. 2004-onwards. InsideWood, Published on the internet: http://insidewood/lib.ncsu.edu/search [01-10-2006]

White, F. 1962. Geographic variation and speciation in Africa with particular reference to *Diospyros*. *Syst. Assoc. Publ.* 4: 71-103.

Wilde, W. J. J. O. de & Duyfjes, B. E. E. 2006. Redefinition of *Zehneria* and four new related genera (Cucurbitaceae), with an enumeration of the australasian and pacific species. *Blumea* 51: 1-88.

Westra, L. Y. T. & Koek-Noorman, J. 2003. Hand Lens Aspects of Annonaceous Wood. *Annonaceae Newsletter* 14: 23-34.

Wijninga, V. M. 1996. Neogene ecology of the Salto de Tequendama site (2475 m altitude, Cordillera Oriental, Colombia): the paleobotanical record of montane and lowland forests. *Rev. Palaeobot. Palynol.* 92: 97-156.

Wikström, N., Savolainen, V. & Chase, M. W. 2001. Evolution of the angiosperms: calibrating the family tree. *Proc. Roy. Soc. Lond. Biol.* 1482: 2211-2220.

Wilkinson, M. 1990. A commentary on Ridley's cladistic solution to the species problem. *Biol. Philos.* 5: 433-446.

Willis, K. J. & McElwain, J. C. 2002. *The evolution of plants*. Oxford University Press, Oxford.

Wilson, E. O. 2000. A global biodiversity map. *Science* 289: 2279.

Woese, C. R. & Fox, G. E. 1977. Phylogenetic structure of the Prokaryotic domain: the primary kingdoms. *Proc. Natl. Acad. Sci. USA* 74: 5088-5090.

Woese, C. R. 1987. Bacterial evolution. *Microbiol. Rev.* 51: 221-271.

Wolf, P. G., Karol, K. G., Mandoli, D. F., Kuehl, J., Arumuganathan, K., Ellis, M. W., Mishler, B. D., Kelch, D. G., Olmstead, R. G. & Boore, J. L. 2004. The first complete chloroplast genome sequence of a lycophyte, *Huperzia lucidula* (Lycopodiaceae). *Gene* 350: 117-128.

Wolfe, K. H. 1991. Protein coding genes in chloroplast DNA: compilation of nucleotide sequences, data base entries, and rates of molecular evolution. Pp. 467-482 in: Vasil, K., (Ed.), *Cell culture and somatic cell genetics of plants*, vol. 7B. Academic press, Inc, San Diego.

Wolfe, K. H., Morden, C. W. & Palmer, J. D. 1992. Function and evolution of a minimal plastid genome from a nonphotosynthetic parasitic plant. *Proc. Natl. Acad. Sci. USA* 89: 10648-10652.

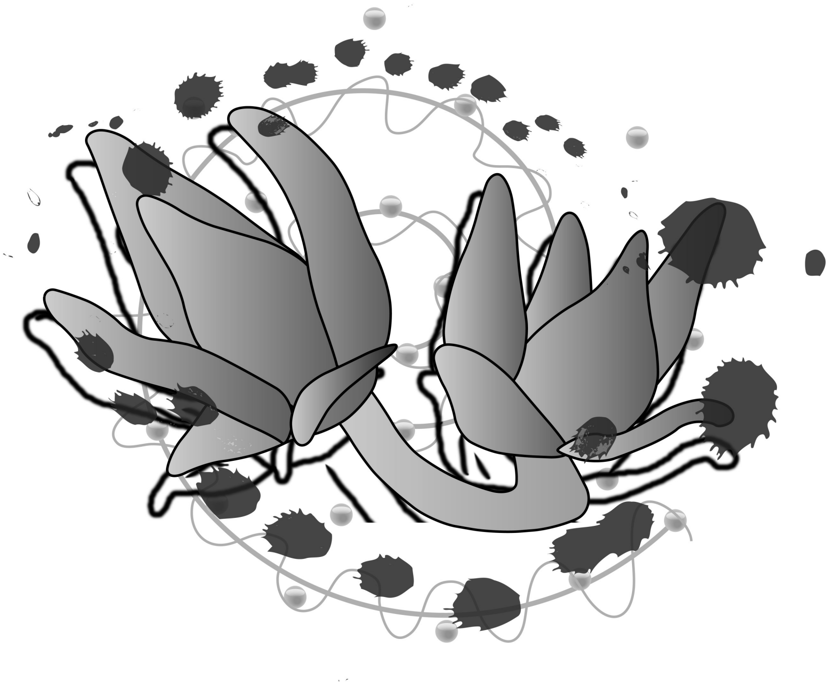
Yang, D. Y., Eng, B., Waye, J. S., Dudar, J. C. & Saunders, S. R. 1998. Improved DNA extraction from ancient bones using silica-based spin columns. *Am. J. Phys. Anthropol.* 105: 539-543.

Yang, Z. 1996. Phylogenetic analysis using parsimony and likelihood methods. *J. Mol. Evol.* 42: 294-307.

Yule, G. U. 1924. A mathematical theory of evolution, based on the conclusions of Dr. J.C. Willis. *Phil. Trans. R. Soc. Lond. B* 213: 21-87.

Zamora V., N., Jiménez M., Q. & Poveda A., L. J. 2000. *Árboles de Costa Rica, Vol. II.* Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

Zeng, Q., Hansson, P. & Wang, X. 2005. Specific and sensitive detection of the conifer pathogen *Gremmeniella abietina* by nested PCR. *BMC Microbiol.* 5: 65-74.



9 SEVEN TAXONOMIC DISCOVERIES FROM SOUTHEASTERN CENTRAL AMERICA

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George E. Schatz[3] & Nelson Zamora[4]

ABSTRACT

During fieldwork in Costa Rica and Panama five, undescribed species of *Guatteria* and one new species of *Desmopsis* were collected and are described here. Additionally, a poorly known species of *Pseudomalmea* is described.

Key words: Annonaceae, *Desmopsis*, *Guatteria, Pseudomalmea*, Costa Rica, Panama, endemics.

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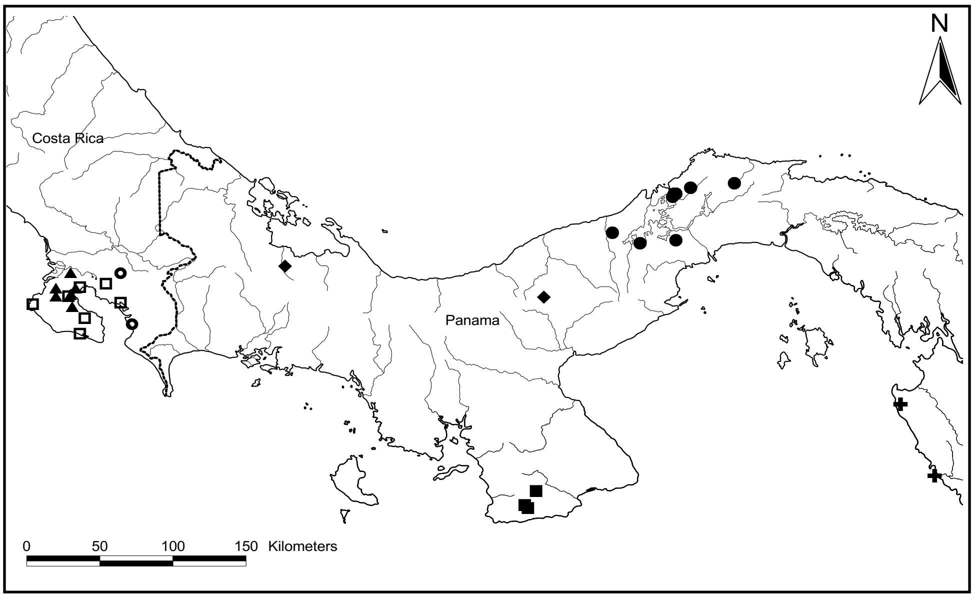
INTRODUCTION

Guatteria (Annonaceae) is a large genus of neotropical trees, comprising approximately 265 species (Chatrou & al., 2004). Ruiz and Pavón described the genus as early as 1794 (Ruiz and Pavón, 1794) but the last and only revision dates back to Fries (1939). The genus itself is easily recognised by its impressed primary vein on the upper side of the leaf, valvate sepals, almost always imbricate petals, numerous carpels (with a single basal ovule), and a pedicel with a distinct suprabasal articulation. The species of *Guatteria*, however, are very homogeneous in many morphological characters, such as habit, flower shape, and number of monocarps. This makes it difficult to understand the systematics and evolution of the genus. Phylogenetic analyses (Erkens & al., in prep.) based on four plastid markers show that *Guatteria* is monophyletic and that most of the endemic Central American *Guatteria* species form a monophyletic group. In order to understand the evolutionary history of these Central American species better, fieldwork in Costa Rica and Panama was carried out by Paul Maas, Hiltje Maas-van de Kamer, and Roy Erkens of the National Herbarium of the Netherlands, Utrecht University branch, and Nelson Zamora, curator of the herbarium of the Instituto Nacional de Biodiversidad (INBio), Santa Domingo de Heredia, Costa Rica, during the months of May and June 2004. With regard to *Guatteria*, Costa Rica has been well collected but in Panama there are many undercollected areas. Material of many *Guatteria* species was collected during this trip, including five unnamed species, which are described here.

Additionally, a new species of *Desmopsis* and a new species in *Pseudomalmea* are described. The new species of *Desmopsis* was collected by Lars Chatrou & al. on a previous collecting trip to Costa Rica. Its name, *D. verrucipes*, was recognised already by Zamora & al. (2000) and is validated here.



Map 1. Distribution of *Guatteria aberrans* Erkens & Maas (●), *Guatteria acrantha* Erkens & Maas (■), *Guatteria reinaldii* Erkens & Maas (⭘), *Guatteria rostrata* Erkens & Maas (▲), *Guatteria zamorae* Erkens & Maas (◆), *Desmopsis verrucipes* Chatrou, Schatz & Zamora (☐), and *Pseudomalmea darienensis* Chatrou (+) in Costa Rica and Panama.

MATERIALS AND METHODS

Herbarium material was investigated from the following herbaria: CR, DUKE, F, GH, INB, K, MO, NY, PMA, SCZ, TEX, U, USJ, and WIS. Measurements as a rule were made on dried material. Measurements on material in spirit are given between accolades { }. Colour indications and descriptions of surface structures are based on dried material, unless stated otherwise. We indicate the density of the indument by using the following gradations: densely, rather densely, and sparsely.

DESCRIPTION OF SPECIES

GUATTERIA

1. Guatteria aberrans Erkens & Maas, *spec. nov.* – Fig. 1, 2; Map 1

Guatteria alabastris acutis *G. pannosae* proxima, sed foliis anguste ellipticis vel anguste ovatis nec anguste oblongis vel raro ellipticis et indumento densiore distincta. – Typus: *Maas, Erkens, Maas-van de Kamer, Zamora* & *Pérez 9570* (holo U; iso INB, K, MO, PMA, SCZ), Panama, Colón, Santa Rita Ridge, Parcela 31 of CTFS, 250 m, 9 June 2004.

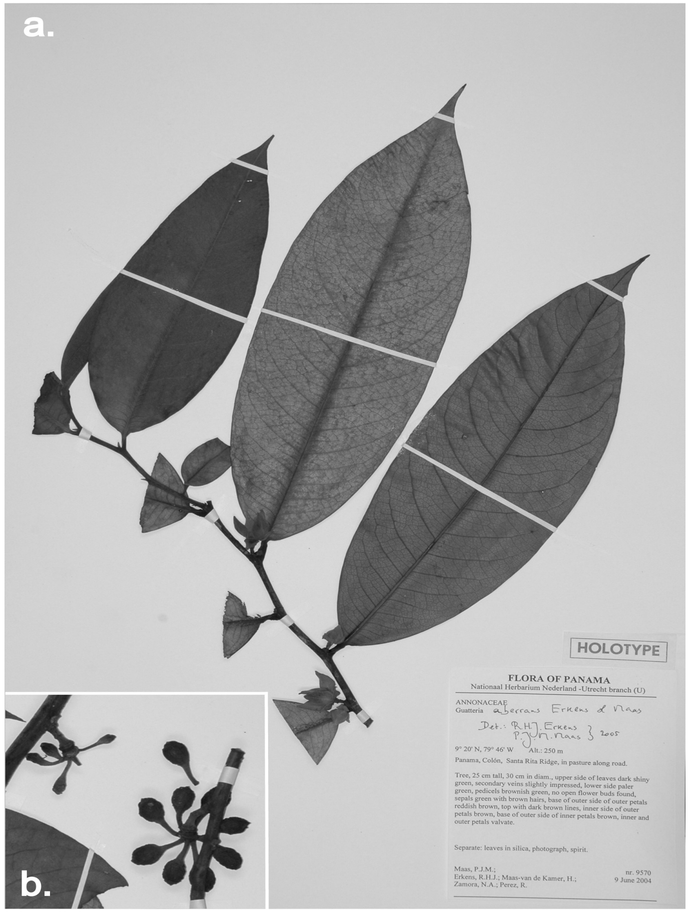
Tree 8-25 m tall, trunk 10-30 cm diam.; young twigs densely covered with erect, curly, brown hairs, soon glabrous. *Leaves*: petiole 5-10 mm long, 2-3 mm diam., decurrent as prominent ridge in young twigs; lamina narrowly elliptic to sometimes narrowly ovate, 15-32 by 4-9.5 cm (leaf index 2.9-3.7), coriaceous, not verrucose, shiny above in vivo, dark blackish brown to grey above, brown to pale brown below, sparsely covered with appressed hairs above, soon glabrous, sparsely covered with appressed hairs below, base obtuse, sometimes slightly attenuate, apex acuminate (acumen 10-15 mm long), secondary veins distinct, 15-18 on either side of primary vein, prominent above, angles with primary vein 45-60°, loop-forming at almost right angles, smallest distance between loops and margin 3-4 mm. *Flowers* solitary or in pairs; pedicels 7-10 mm long, 1-2 mm diam., fruiting pedicels 9-12 mm long, 2-3 mm diam., densely covered with erect, curly, brown hairs; flower buds ovoid, distinctly apiculate; sepals free, triangular to very broadly triangular, 7-10 by 5-8 mm, patent but soon becoming completely reflexed, outer side densely covered with erect, curly, brown hairs; petals brown to chocolate-coloured in vivo, unequal, outer ones narrowly elliptic, basal margins reflexed outwards, 13-20{-32} by 5-7{-9} mm, inner ones valvate, narrowly triangular-ovate, base thickened and almost spur-like, bifacial (as in the genus *Anaxagorea*) above the middle, 15-20{-32} by 7-8{-13} mm, outer side densely covered with erect, curly, brown hairs; stamens c. 1.5 mm long, connective shield glabrous. *Monocarps* 10-40, young monocarps green in vivo, blackish in sicco, ellipsoid, 10-14 by 7-9 mm, sparsely covered with erect, curly, brown hairs, soon glabrous, apex minutely apiculate (apicle < 0.5 mm long), wrinkled in sicco, stipes 9-14 by 1-2 mm, densely covered with erect, curly, brown hairs. *Seed* ellipsoid, 10-12 by 5-6 mm, smooth.

Distribution – Panama (Comarca de San Blas, Colón).

Habitat & Ecology – Forest, sometimes along roadsides. At elevations from sea level up to 250 m.

Phenology – Flowering: February, June, and July ; fruiting: February and June.

Notes – *Guatteria aberrans* is strongly deviating from other species of *Guatteria*, except *G. pannosa* Scharf & Maas, by its pointed flower buds and by its valvate, almost spurred inner



FLORA OF PANAMA
Nationaal Herbarium Nederland -Utrecht branch (U)

ANNONACEAE
Guatteria aberrans Erkens & Maas

Det.: R.H.J. Erkens
P.J.M. Maas } 2005

9° 20' N, 79° 46' W Alt.: 250 m

Panama, Colón, Santa Rita Ridge, in pasture along road.

Tree, 25 cm tall, 30 cm in diam., upper side of leaves dark shiny green, secondary veins slightly impressed, lower side paler green, pedicels brownish green, no open flower buds found, sepals green with brown hairs, base of outer side of outer petals reddish brown, top with dark brown lines, inner side of outer petals brown, base of outer side of inner petals brown, inner and outer petals valvate.

Separate: leaves in silica, photograph, spirit.

Maas, P.J.M.;
Erkens, R.H.J.; Maas-van de Kamer, H.;
Zamora, N.A.; Perez, R.

nr. 9570
9 June 2004

Figure 1. *Guatteria aberrans* Erkens & Maas. a. Flowering twig; b. (inset) fruiting twig (a: *Maas & al. 9570*; b: *Maas & al. 9564*).

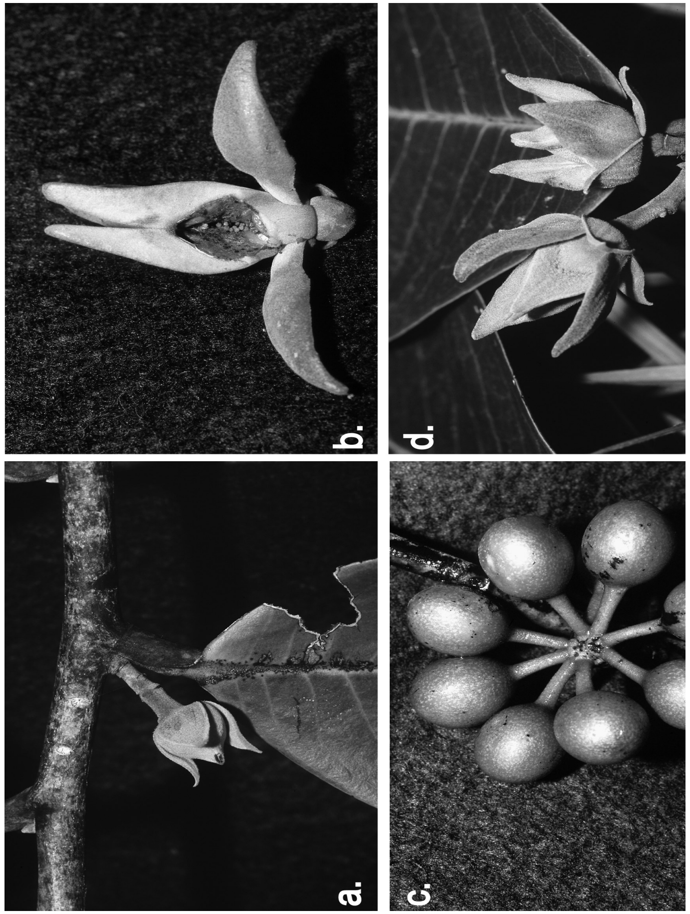


Figure 2. *Guatteria aberrans* Erkens & Maas. a. Flower; b. longitudinal section of flower; c. fruit; d. inflorescence (a, c: *Maas & al. 9564;* b, d: *Maas & al. 9570*).

petals. Another peculiarity of this species is that the inner petals seem to stay closed during the whole life cycle (no open bud development seen). *Cogollo & Brand 373* (MO) from Colombia, Antioquia, Mun. San Luis, Highway Medellín – Bogotá, 2 km from Río Claro, near Río Samaná, alt. 790m, probably belongs to this species. It matches *G. aberrans* in almost all aspects (pointed flower buds, leaf size, and flower size). Its flowers are annotated as pink ("rosada") and its fruits as black.

G. pannosa, recently described from French Guiana and adjacent Brazil (Amapá; Scharf, Maas & Morawetz, 2005), shows a striking similarity in flower architecture. On the basis of other characters, however, it is fairly easy to distinguish both species (table 1), and therefore *G. aberrans* is described as new. Its relationship to other species of *Guatteria* is unknown so far.

Etymology – This species is so named because of its aberrant flower type in comparison to the majority of *Guatteria* flowers or flower buds.

Paratypes:

PANAMA. Colón: *Aizprúa & Araúz 3375* (SCZ, U), Santa Rita Ridge, road to Agua Clara, 190 m; *Aranda 3022* (SCZ, U), Santa Rita; *Galdames & al. 4473* (SCZ, U), road to Sierra Llorona; *Luque & al. 509* (PMA, U), Santa Rita; *Luque & al. 566* (PMA, U), La Llana, Parque Nacionál Chagres; *Maas, Erkens, Maas-van de Kamer, Zamora & Pérez 9564* (INB, PMA, SCZ, U), Santa Rita Ridge, 200 m. Comarca de San Blas: *de Nevers & Herrera 7168* (MO, U), Cangandi, 30 m.

2. Guatteria acrantha Erkens & Maas, *spec. nov.* – Fig. 3, 4; Map 1

Guatteria floribus terminalibus pro ratione parvis, foliis parvis apice rotundatis distincta. – Typus: *Rivera 355* (holo SCZ; iso PMA, U), Panama, Los Santos, Distr. Tonosí, Cerro Los Piraguales, El Cortezo, 900 m, 20 Apr. 1994.

Tree or shrub 5-20 m tall; young twigs sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 1-3 mm long, 1 mm diam.; lamina narrowly obovate to narrowly elliptic, 5-8 by 2-3.5 cm (leaf index 2.2-2.8), chartaceous, not verrucose, dull dark brown above, brown to brownish green below, glabrous above, rather densely covered with appressed hairs below, base attenuate, apex rounded or sometimes very shortly and bluntly acuminate, secondary veins distinct, 6-9 on either side of primary vein, flat to slightly raised above, angles with primary vein 60-70°, loop-forming at right to obtuse angles, smallest distance between loops and margin 1-2 mm. *Flowers* solitary, terminal; pedicels 6-12 mm long, c. 1 mm diam., densely covered with appressed, brown hairs; flower buds broadly ovoid-deltoid; sepals free, ovate-triangular to deltate, 3-5 by 3-4 mm, appressed to reflexed, outer side densely covered with appressed, brown hairs; petals greenish in vivo, subequal, obovate, 7-9 by 5-7 mm, outer side densely covered with appressed, brown hairs; stamens 1-1.5 mm long, connective shield papillate. *Monocarps* c. 10, green in vivo, black in sicco, narrowly ellipsoid, 7-10 by 3-4 mm, subglabrous, apex apiculate (apicle c. 1 mm long), stipes black, 1-2 by 1 mm, subglabrous. *Seed* narrowly ellipsoid, c. 8 by 3 mm, pale brown, pitted.

Distribution – Panama (Veraguas and Los Santos).

Habitat & Ecology – Cloud forest. At elevations of 900-1500 m.

Phenology – Flowering: February to April; fruiting: April.

Notes – *Guatteria acrantha* is very well characterised by having terminal flowers, in combination with very small flowers for the genus (only 15-20 mm diam., petals < 10 mm long) and small leaves with a mostly rounded apex. Superficially, it looks similar to *G. rotundata* Maas & Setten by the shape of its leaves, but it is quite distinct by having terminal flowers. The only other Central American species of *Guatteria* with terminal flowers is *Guatteria grandiflora* Donn. Sm. (incl. *Guatteria anomala* R.E. Fr.), a species occurring in Mexico, Guatemala, and Honduras, but the latter species has much larger flowers (petals 22-42 mm long) and leaves (5.5-22 x 2-7 cm).
Etymology – From "akros" (top) and "anthos" (flower), referring to the terminal flower, the distinguishing feature of this new species.

Paratypes:
PANAMA. Veraguas: *Deago & al. 265* (PMA, SCZ), Distr. Montijo, Cerro Hoya, ascending to Cobachón; *Deago & al. 371* (U), Distr. Montijo, Cerro Hoya, ascending to Río Pedregal, 1500 m.

Table 1. morphological differences between *G. aberrans* Erkens & Maas (Panama) and *G. pannosa* Scharf & Maas (French Guiana, Brazil).

	G. aberrans	*G. pannosa*
Petiole	decurrent into the young twigs as a protruding edge	not decurrent
Leaf base	obtuse	acute
Lamina	narrowly elliptic or sometimes narrowly ovate; 15-32 by 4-9.5 cm	narrowly oblong, rarely narrowly elliptic; 10-20 by 2.5-4 cm
Lower side leaf	sparsely covered with appressed hairs	densely covered with appressed hairs
Stipe length	9-14 mm	20-25 mm

3. Guatteria reinaldii Erkens & Maas, *spec. nov.* – Fig. 5; Map 1

Guatteriae pudicae proxima, sed foliis leviter falcatis, venis secundariis paucioribus differt. – Typus: *Aguilar & al. 2031* (holo INB; iso U), Costa Rica, Puntarenas, Cantón de Osa, Fila Costena, 2 km N of Piedras Blancas, near Cerro Anguciana, 900 m, 28 Jul. 1993.

Tree 4-10 m tall, trunk c. 12 cm diam.; young twigs rather densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2-4 mm long, 1-2 mm diam.; lamina narrowly ovate to narrowly elliptic and slightly falcate, 13-20 by 4-6 cm (leaf index 2.8-3.3), chartaceous, sparsely or not verrucose above, shiny above, greyish green on both sides, glabrous above, but primary vein densely covered with appressed to erect hairs (primary vein may look verrucose by remaining hair bases), sparsely to rather densely covered with appressed hairs below, base obtuse, apex acuminate (acumen 10-15 mm long), secondary veins distinct, 6-10 on either side of primary vein, strongly prominent above, angles with primary vein 60-65°, loop-forming at right to obtuse angles, smallest distance between loops and margin 3-5 mm. *Flowers* solitary or in pairs; pedicels 3-5 mm long, c. 1 mm diam., fruiting pedicels to 7 mm long, to 3 mm diam., densely covered with appressed, dark brown hairs; sepals free, deltate, c. 6 by 6 mm, appressed, outer side densely covered with appressed, dark brown hairs; petals cream in vivo, subequal, broadly ovate-triangular, 8-14 by 8-11 mm, outer side densely covered with appressed, dark brown hairs; stamens 2-2.5 mm long,

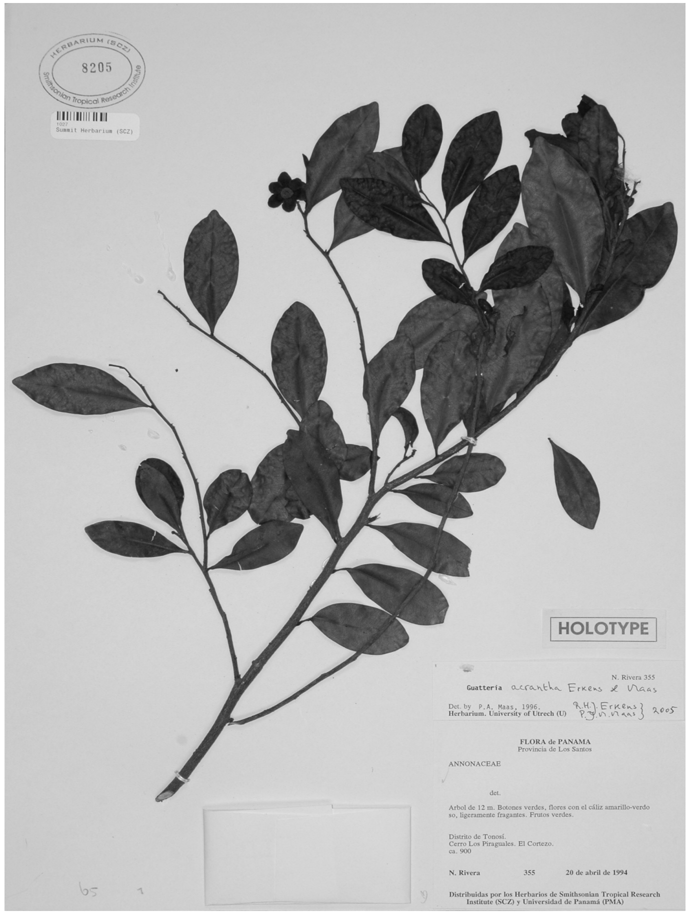


Figure 3. *Guatteria acrantha* Erkens & Maas. Flowering branch (*Rivera 355*).

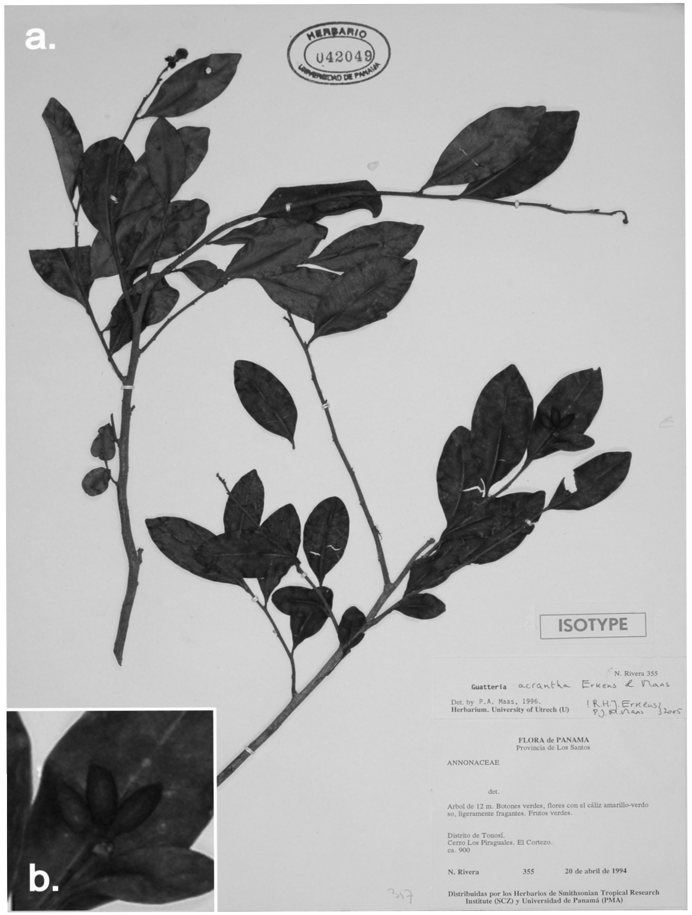


Figure 4. *Guatteria acrantha* Erkens & Maas. a. Flowering and fruiting twig; b. close-up of fruit (a, b: *Rivera 355*).

Figure 5. *Guatteria reinaldii* Erkens & Maas. a. Flowering and fruiting twig; b. close-up of fruit and flowers (a, b: *Aguilar & al. 2031*).

Table 2. morphological differences between *G. reinaldii* Erkens & Maas (Costa Rica) and *G. pudica* N. Zamora & Maas (Costa Rica).

	G. reinaldii	*G. pudica*
Indument of young twigs	densely covered with appressed hairs	densely covered with erect hairs
Petiole	2--4 by 1--2 mm	5--8 by 3 mm
Leaf base	obtuse	acute
Lamina	narrowly elliptic, slightly falcate; 15--32 by 4--9.5 cm	narrowly oblong, rarely narrowly elliptic, symmetrical; 10--20 by 2.5--4 cm
Secondary veins	6--10	10--20
Lower side of leaf	sparsely to rather densely covered with appressed hairs	densely covered with erect hairs
Pedicel length	3--7 mm	10--17 mm
Stipe length	1--3 mm	5--10 mm
Monocarps	< 10, narrowly ellipsoid, 10--14 by 4--8 mm	30--40, ellipsoid, 8--11 by 4--6 mm

connective shield papillate. *Monocarps* <10, purple-black in vivo, black in sicco, narrowly ellipsoid, 10-14 by 4-8 mm, sparsely covered with appressed hairs, apex rounded or apiculate, stipes 1-3 by 1 mm, sparsely covered with appressed hairs. *Seed* ellipsoid, c. 10 by 6 mm, pale brown, slightly pitted.

Distribution – Costa Rica (Puntarenas, Osa Peninsula).

Habitat & Ecology – Forest. At an elevation of 900 m.

Phenology – Flowering: July and December; fruiting: July.

Notes – This species at first sight resembles *G. pudica* N. Zamora & Maas but its parts are generally smaller in size (table 2). Both species occur in the Osa area and probably are closely related.

Etymology – This species is named after Reinaldo Aguilar, an independent botanical field researcher in the Osa Peninsula (Costa Rica), who made many important general collections of Annonaceae.

Paratypes:

COSTA RICA. Puntarenas: *Aguilar & al. 4810* (INB), Canton Osa, Serranías de Golfito, Piedras Blancas, 100 m.

4. Guatteria rostrata Erkens & Maas, *spec. nov.* – Fig. 6, 7; Map 1

Guatteria amplifoliae proxima, sed monocarpiis rostratis distincta. – Typus: *Aguilar & al. 3654* (holo U; iso CR, INB), Costa Rica, Puntarenas, Canton Osa, Reserva Forestal Golfo Dulce, near Rancho Quemado, 200-350 m, 1 Nov. 1994.

Tree 7-20 m tall, trunk 20-60 cm diam., black or grey; young twigs densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 15-20 mm long, 2-3 mm diam.; lamina elliptic to obovate or narrowly so, 18-28 by 7-11 cm (leaf index 2.4-2.6), chartaceous, not verrucose, dull, greyish brown above, brown below, glabrous above, rather densely covered with appressed hairs below, base attenuate into a narrowly winged petiole, apex acuminate (acumen 10-20 mm long), secondary veins distinct, 16-19 on either side of primary vein, impressed above in vivo, raised above in sicco, angles with primary vein 60-70°, loop-forming at right to obtuse angles, smallest distance between loops and margin 3-6 mm. *Flowers* solitary or in pairs; pedicels 15-35 mm long, c. 1 mm diam., fruiting pedicels to 2 mm diam., densely covered with appressed hairs, finally subglabrous; flower buds very broadly ovoid; sepals free, triangular, 7-12 by 5-10 mm, patent, outer side rather densely covered with appressed hairs; petals green to yellowish green in vivo, unequal, outer ones ovate, 14-22 by 10-15 mm, inner ones oblong-elliptic to ovate, 10-15 by 5-9 mm, outer side densely covered with appressed hairs; stamens c. 2 mm long, connective shield densely papillate. *Monocarps* 5-15, green, maturing red to purple-black in vivo, black in sicco, narrowly ellipsoid, 15-18 by 6-7 mm, sparsely covered with erect hairs, soon glabrous, apex rostrate (beak 1-2 by 1-2 mm), stipes 7-10 by 1 mm, sparsely covered with appressed hairs, soon glabrous. *Seed* ellipsoid, apex slightly pointed, c. 15 by 7 mm, pale brown, slightly tuberculate.

Distribution – Costa Rica (Puntarenas, Osa District).

Habitat & Ecology – Forest. At elevations from sea level up to 350 m.

Phenology – Flowering: May and July; fruiting: February, May, June, and November.

Notes – In the field *Guatteria rostrata* is easily recognised by its black or grey trunk,

Figure 6. *Guatteria rostrata* Erkens & Maas. a. Fruiting twig; b. (inset) flowering twig (a: *Aguilar & al. 3654*; b: *Aguilar 4611*).

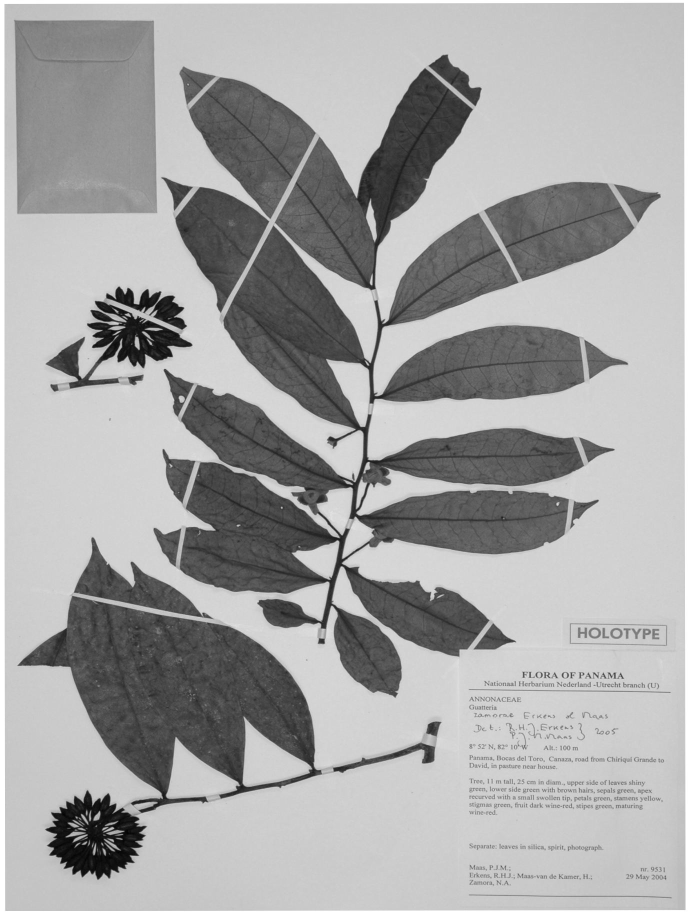
Figure 7. *Guatteria rostrata* Erkens & Maas. a. Twig with young flower buds; b. close-up of inflorescence; c. open and closed flower buds; d. fruit (a, b, d: *Maas & al. 9497*; c: *Maas & al. 9493*).

sometimes with narrow buttresses reaching up to 8 m (*Hammel 16960*). In the field this species superficially resembles *G. amplifolia* Triana & Planch somewhat because of its large leaves. In *G. rostrata*, however, the petiole is generally somewhat longer (15-20 by 2-3 mm versus 4-10 by 4-6 mm). Moreover, the monocarps of *G. rostrata* are 5-15 in number, 15-18 by 6-7 mm and rostrate, while *G. amplifolia* has more monocarps (20-40), which are shorter (8-10 by 5-6 mm), and ellipsoid to pyriform, lacking the rostrate apex.
Etymology – This species is named "rostrata" after its beaked (=rostrate) monocarps.

Paratypes:
COSTA RICA. Puntarenas: *Hammel & al. 16960* (CR, INB), Canton Osa, Reserva Forestal Golfo Dulce, near Rancho Quemado, 200 m; *Aguilar & al. 4611* (CR, INB, U), Canton Osa, Reserva Forestal Golfo Dulce, Bahia Chal, 150 m; *Chatrou & al. 118* (CR, INB, U), idem, 175 m; *Maas, Erkens, Maas-van de Kamer, Rodríguez & Alfaro 9493* (CR, INB, K, NY, U), Canton Osa, Distr. Rincón, 2 km before Banejas, 75 m; *Maas, Erkens, Maas-van de Kamer, Rodríguez & Alfaro 9497* (CR, INB, U), Canton Osa, Distr. Puerto Jiménez, Guadeloupe de La Palma, 100 m.

5. Guatteria zamorae Erkens & Maas, *spec. nov.* – Fig. 8, 9; Map 1
Guatteria foliis in sicco ochraceis et verrucosis, monocarpiis apiculatis distincta. – Typus: *Maas, Erkens, Maas-van de Kamer & Zamora 9531* (holo U; iso INB, K, MO, NY, PMA, SCZ), Panama, Bocas del Toro, Canaza, road from Chiriquí Grande to David, 100 m, 29 May 2004.

Tree 11-15 m tall, trunk 25-30 cm diam.; young twigs densely covered with erect, brown hairs, finally glabrous. *Leaves*: petiole 3-9 mm long, 1-2 mm diam.; lamina narrowly obovate to narrowly elliptic, 10-17 by 3-5 cm, chartaceous, rather densely to densely verrucose above, greenish brown above, yellowish brown below, glabrous above except for the densely hairy primary vein and secondary veins, densely covered with erect, brown hairs below, base acute, apex acuminate (acumen 5-10 mm long), secondary veins distinct, 10-15 on either side of primary vein, prominent above, angles with primary vein 55-65°, loop-forming at right to obtuse angles, smallest distance between loops and margin 2-3 mm. *Flowers* solitary; pedicels 25-30 mm long, 1-1.5 mm diam., fruiting pedicels up to 35 mm long, up to 2 mm diam., densely covered with erect hairs; flower buds depressed ovoid, apiculate; sepals free, very broadly ovate-triangular, 4{-8} by 4-5{-8} mm, patent, extreme apex rolled inwards and thickened, outer side rather densely to densely covered with appressed and erect hairs; petals green to greyish green in vivo, subequal, ovate to ovate-oblong, 10-12{-18} by 5-7{-10} mm, outer side densely covered with appressed and erect hairs; stamens yellow, connective shield densely papillate. *Monocarps* 30-50, green, maturing dark wine-red in vivo, black in sicco, ellipsoid, 9-12{-15} by 4-5{-7} mm, glabrous except for some scattered hairs near the apex, apex apiculate (apicle 1-2 mm long) in dry material, rounded in fresh material, stipes green, maturing dark wine-red in vivo, 6-10 by 1{-2} mm. *Seed* narrowly ellipsoid, 8-10 by 3-4 mm, tuberculate.
Distribution – Panama (Coclé).
Habitat & Ecology – Forest and pasture. At elevations of 100 and 750 m.
Phenology – Flowering and fruiting: May.
Notes – *Guatteria zamorae* can easily be distinguished from the other Central American species of *Guatteria* by the yellowish brown leaf colour after drying, its verrucose leaves,



FLORA OF PANAMA
Nationaal Herbarium Nederland -Utrecht branch (U)

ANNONACEAE
Guatteria
zamorae Erkens & Maas
Det.: R.H.J. Erkens } 2005
P.J.M. Maas }
8° 52' N, 82° 10' W Alt.: 100 m

Panama, Bocas del Toro, Canaza, road from Chiriquí Grande to David, in pasture near house.

Tree, 11 m tall, 25 cm in diam., upper side of leaves shiny green, lower side green with brown hairs, sepals green, apex recurved with a small swollen tip, petals green, stamens yellow, stigmas green, fruit dark wine-red, stipes green, maturing wine-red.

Separate: leaves in silica, spirit, photograph.

Maas, P.J.M.; nr. 9531
Erkens, R.H.J.; Maas-van de Kamer, H.; 29 May 2004
Zamora, N.A.

Figure 8. *Guatteria zamorae* Erkens & Maas. Flowering and fruiting twigs (*Maas & al. 9531*).

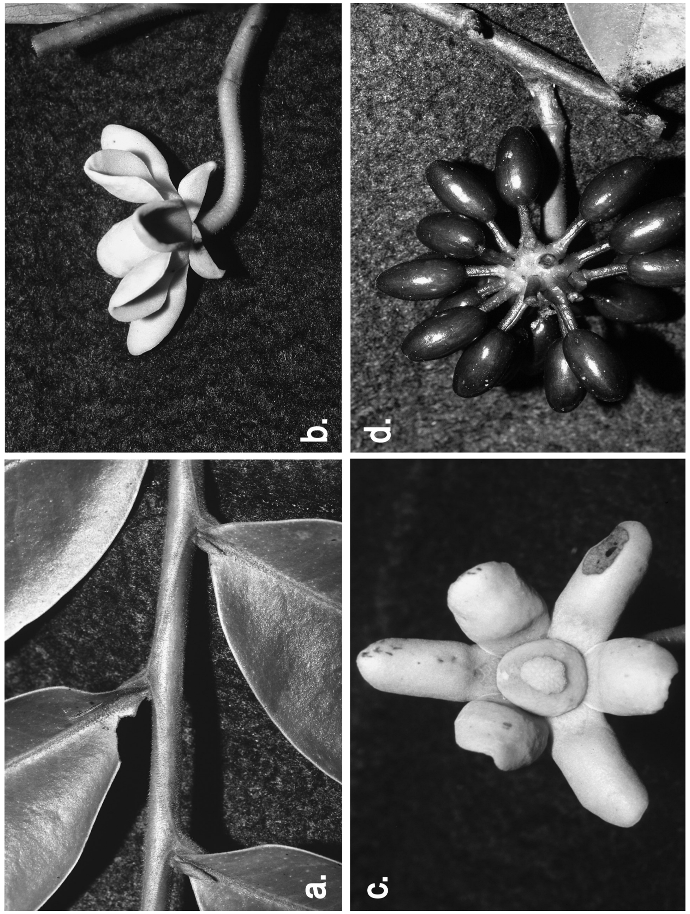


Figure 9. *Guatteria zamorae* Erkens & Maas. a. Leafy twig; b. open flower bud, side view; c. open flower bud, inside view; d. mature fruit (a-d: *Maas & al. 9531*).

and apiculate monocarps. Preliminary unpublished phylogenetic analyses suggest that this species belongs to a group comprising three Central American species, namely *G. talamancana* Zamora & Maas, *G. oliviformis* Donn. Sm., and *G. allenii* R.E. Fr. Two bracts were seen around the flower buds, both triangular, one 4{-6} by 3{-4} mm and the other 5{-8} by 4{-5} mm. This is interesting because *G. talamancana* is known for its very large bracts (25-30 mm) on the pedicel. The latter, however, has a thick brown indument all over the leaf, while *G. zamorae* only has densely hairy primary and secondary veins.

Measurements taken from spirit material of stipes gave a smaller length than that from dried material, namely 3-5 mm long.

Etymology – This species is named after Nelson Zamora, the curator of the Herbarium of INBio (Instituto Nacional de Biodiversidad) in Costa Rica, without whom this field trip would have been impossible. The authors greatly acknowledge his help in providing fieldwork gear, a car, and a tremendous good eye for spotting Annonaceae species in the field. He himself went through great trouble in collecting this new species with the aid of a crossbow.

Paratypes:
PANAMA. Coclé: *Maas, Erkens, Maas-van de Kamer, Zamora & Navas 9542* (INB, PMA, SCZ, U), Parque Nacional General Omar Torijos Herrera, El Copé, Sendero Rana Dorada, 750 m.

DESMOPSIS

Desmopsis verrucipes Chatrou, G.E. Schatz & N. Zamora, *spec. nov.* – Fig. 10; Map 1
Haec species inflorescentia ut apparet thyrsoidea, pedicellis verrucosis en sepalis magnis persistentibus distincta est – Typus: *Chatrou, Oosterhof & Aguilar 102* (holo U; iso CR, INB, MO), Costa Rica, Puntarenas, Cantón Osa, 5 km from Bahia Chal, near mouth of Río Rincón, 50 m, 29 November 1998.

Treelet to 8 m tall, trunk 2-4 cm diam.; young twigs, below sparsely covered with appressed, yellowish brown hairs 0.1-0.2(-0.4) mm long. *Leaves*: petiole 5-13 mm long, (1-)2 mm diam., canaliculate, drying dark; lamina narrowly elliptic to elliptic, often slightly falcate and slightly asymmetric, 13-32 by 4.5-12.5 cm, chartaceous, densely verruculose on both sides, olive green on both sides, petioles, both sides of primary vein, and margin of leaf blade below sparsely covered with appressed, yellowish brown hairs 0.1-0.2(-0.4) mm long, base narrowly to broadly cuneate, apex acuminate (acumen 5-20 mm long), primary vein impressed above, secondary veins 7-14 on either side of primary vein, raised above, irregularly spaced, curving upwards, angles with primary vein (35-)55-60(-75)°, only weakly loop-forming at acute to right angles, smallest distance between loops and margin 2-6 mm. *Inflorescences* essentially terminal, but mostly pseudolateral due to overtopping by the axillary shoot, and often appearing along internodes on slightly older, leafless branches, thyrsoids with mostly two rhipidia, central axis 3-6 mm long, 1-3 mm diam., axial internodes 1-3 mm long, rhipidia up to 3-flowered (including flower buds); peduncles, pedicels, and bracts sparsely to rather densely covered with brown, appressed hairs 0.1-0.2 mm, articulation of pedicel clearly visible as a ring of hairs 1-3 mm above lower bract, subtending the pedicel, uppermost bract at 1/3 from base of pedicel; bracts depressed ovate, semi-amplectent, c. 2 mm by c. 4 mm, pedicels 8-19 by 1-3 mm (to 7 mm in fruiting stage), vertically striate and verrucose, even more so in fruiting stage; sepals free, maturing red in vivo, foliaceous with visible venation, persistant, often still present in fruit, ovate to triangular, 9-20 by 5-10 mm wide, apex acute, ciliate, verruculose on both sides, outer side rather densely covered with brown, appressed hairs c. 0.2 mm long; petals maturing white in vivo, subequal, narrowly triangular, 15-30 by 5-8 mm, apex acute, inner petals slightly narrower than outer ones, ciliate, outer side rather densely covered with brown, appressed hairs c. 0.2 mm long, inner side glabrous except for apex; stamens 80-150, 1.5-2.0 mm long, filament 0.3 mm long, anther connective shield discoid, 0.1 mm thick, glabrous; carpels 15-25, ovary prismatic, 1.6-2.0 mm long, sparsely covered with short, appressed hairs to glabrous (except for extreme base), stigma globose, c. 0.3 mm diam., totally covered with white hairs 0.1 mm, ovules 4-6 in a single row. *Monocarps* 7-20, maturing yellow in vivo, black in sicco, ellipsoid, 12-29 by 8-14 mm, glabrous, apex rounded, stipes maturing dark red in vivo, 5-12 by 1-2 mm, subglabrous to sparsely covered with brown, appressed hairs c. 0.2 mm long. *Seed* flattened discoid, 8-10 by 2-3 mm, surface smooth, light reddish brown, the raphe a shallow equatorial furrow.

Distribution – Southwestern Costa Rica, known only from the Golfo Dulce area, including the Osa Peninsula.

Habitat & Ecology – Tropical wet forests. At elevations of 0 to 250 m.

Phenology – Flowering: August through November. Fruiting: October through March.

Notes – The verrucose pedicel, the large, persistent sepals, and the thyrsoid inflorescences that usually are borne on older, leafless branches distinguish *D. verrucipes.*

The inflorescences of *D. verrucipes* are described as a thyrsoid in the sense of Weberling & Hoppe (1996), viz. a ramification system with cymosely branched partial inflorescences on a multinodate main axis, which ends in a terminal flower. In this new species, no more than two 'partial inflorescences', rhipidia, have been observed per inflorescence. A peculiar feature of the rhipidia is the fact that successive flowers are not arranged in one plane, i.e. the flowers do not alternate at angles of 180°, but at a much smaller angle. A similar deviation from the usual rhipidiate inflorescence in Annonaceae was reported for *Fusaea* (Chatrou & He, 1999). This publication validates the name *D. verrucipes*, already mentioned by Zamora & al. (2000), Schatz (1987) listed this species provisionally under the name *D. walkeri*.

Etymology – The name of this new species refers to the verrucose pedicel, noticeable in flowering, but especially in fruiting stage.

Paratypes:

COSTA RICA. Puntarenas: *Aguilar 5274* (INB, U), Cantón Golfito, Laguna Pejeperrito, 0 m; *Chatrou, Oosterhof & Aguilar 115* (CR, INB, K, MO, U), Cantón Golfito, Dos Brazos del Tigre, 250 m; *Fonseca 23* (CR, MO), Cantón Osa, Parque Nacional Corcovado, 10 m; *Kernan 282* (MO, U), Parque Nacional Corcovado, 0-150 m; *Kernan 801* (MO), without locality information, 0 m; *Knapp & Mallet 2202* (MO), Parque Nacional Corcovado, ridges above Río Claro, 0-100 m; *Maas, Maas-van de Kamer, Hammel & Chavarría 7839* (INB, U), Cantón Osa, 2 km from Chacarita, S of Palmar Norte; *Neill 5049A* (MO), without locality information, 200 m; *Salas 182* (CR, DUKE, F, GH, MO, WIS), Golfito; *Thomsen 197* (CR, K, U, USJ), Río Riyito, 50 m; *Todzia & Gilbert 1709* (TEX), near edge of Río Sirena; *Walker 193* (CR, F, DUKE, GH, MO, WIS), forest above United Fruit Company's headquarters, 2 km N of Golfito, 10-20 m.

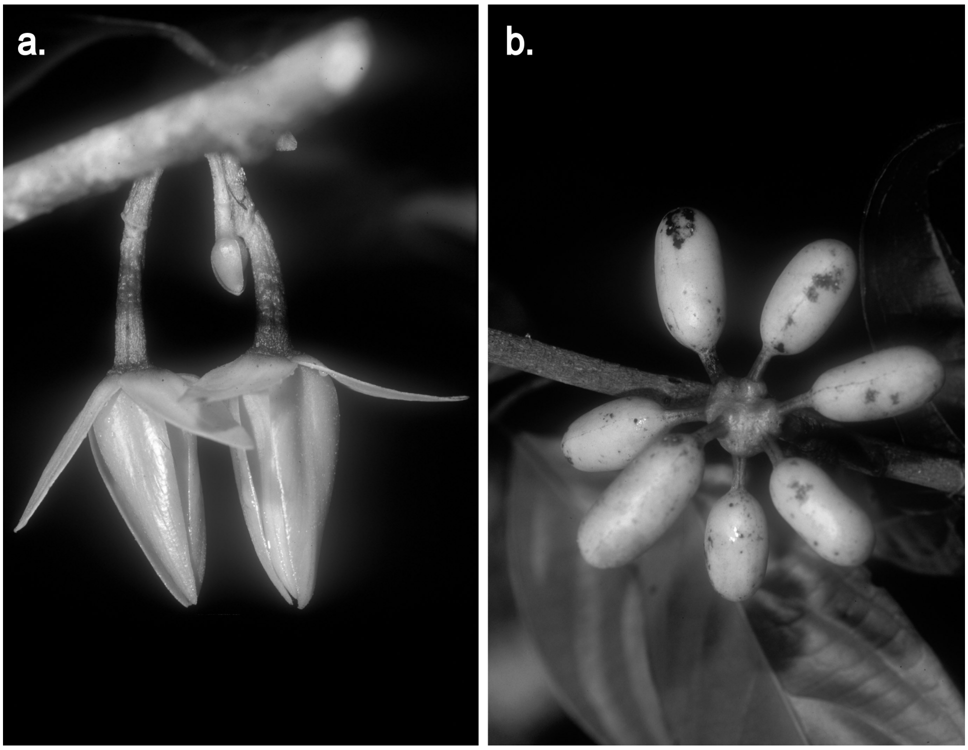


Figure 10. *Desmopsis verrucipes* Chatrou, Schatz & Zamora. a. Immature flowers; b. immature fruit (a: *Chatrou & al. 102*; b: *Chatrou & al. 115*).

PSEUDOMALMEA

Pseudomalmea darienensis Chatrou, *spec. nov.* – Fig. 11; Map 1
A speciebus ceteris in genere *Pseudomalmea* foliis magnis, pedicello bractea supra articulationem instructo et stipite brevi differt. – Typus: *McPherson, Hensold, Palacios, Herrera & Polanco 15345* (holo U; iso MO), Panama, Darién, S of Garachine on W flank of Serranía Sapo, above place called Casa Vieja, 50-150 m, 21 May 1991.

Tree 14-25 m tall, young twigs glabrous. *Leaves*: petiole 4-5 mm long by c. 1.5 mm diam.; lamina narrowly elliptic to ellipic, 12-19 by 4-8 cm, chartaceous, on both sides with uneven light to dark brown patches, petioles, lower side of primary vein, basal part of leaf blade and primary vein below sparsely to rather densely covered with brownish, appressed hairs 0.2-0.6(-0.8) mm long, base (shortly) attenuate, apex gradually acuminate (acumen 5-14 mm long), secondary veins 7-10 per side, irregularly spaced, angles with primary vein 45-70°, indistinctly loop-forming at acute-right angles, distance between loops and leaf margin 3-7 mm, intersecondaries present, tertiary venation reticulate with few percurrents. *Infructescences* on older, leafless branches; pedicels 9-25 by ca. 3 mm basally to c. 4 mm apically, bract above articulation semi-amplectent, c. 1 mm by c. 2.5 mm; pedicels and outer side of bracts rather densely covered with brown, appressed hairs 0.2-0.4(-0.6) mm long.

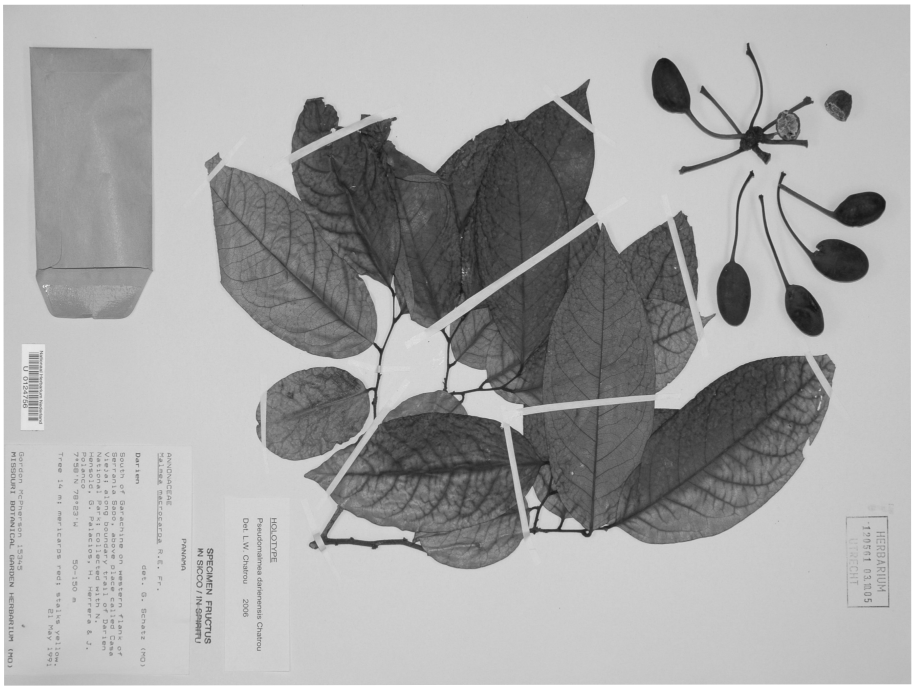


Figure 11. *Pseudomalmea darienensis* Chatrou. Leafy twig and fruit (*McPherson 15345*).

Flowers unknown. *Monocarps* 10-15, red at maturity in vivo, (reddish) brown in sicco, ellipsoid, 18-32 by 11-19 mm, sparsely covered with yellowish brown, appressed to erect hairs 0.2-0.6 mm long, verrucose to rugose, stipes 22-32(-44) by 1-2 mm, sparsely covered with yellowish brown, appressed to erect hairs 0.2-0.6 mm long, fruiting receptacle transversely ellipsoid, 11-15 mm in diam., 6-8 mm high, densely hairy. *Seed* ellipsoid, 16-30 by 9-17 mm, reddish brown, shallowly transversely striate, raphe slightly raised.

Distribution – Panama, only known from two collections made in the province of Darién.

Habitat & Ecology – Tropical wet forest. At elevations of up to 150 m.

Phenology – Fruiting: January through May.

Notes – Despite the availability of two fruiting specimens only, the material clearly represents a new species, and *Pseudomalmea darienensis* is published to further document the rich flora of Panama, and Darién in particular.

Etymology – The name of this new species refers to the Panamanian state of Darién, in which both collections have been made.

Paratype:

PANAMA. Darién: *Garwood, Gibby, Hampshire & Humphries 265* (BM, MO), Ensenada del Guayabo, 18 km SE of Jaqué, 100 m.

KEY TO THE SPECIES OF PSEUDOMALMEA

Pseudomalmea darienensis is the fourth species within the genus, and the first one to be described for Central America. Given the recent doubling of the size of the genus due to the publication of *P. dariensisis* here, and of *P. wingfieldii* (Chatrou & Pirie, 2005), it is appropriate to present a key to the species of *Pseudomalmea* here.

1a. Primary vein on lower side glabrous or uniformly covered with appressed hairs............2
1b. Primary vein on lower side covered with patches of erect hairs..........................*P. boyacana*

2a. Pedicel above articulation with a single bract..3
2b. Pedicel above articulation without a bract...*P.wingfieldii*

3a. Lower side of leaves subglabrous, fruiting receptacle glabrous, stipes and monocarps subglabrous, stipes 45-75 mm long..*P. diclina*
3b. Lower side of leaves sparsely to rather densely hairy, fruiting receptacle densely hairy, stipes and monocarps sparsely hairy, stipes 22-32(-44) mm long..........................*P. darienensis*

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REFERENCES

Chatrou, L. W. & He, P. 1999. Studies in Annonaceae XXXIII. A revision of Fusaea (Baill.) Saff. *Brittonia* 52: 181-203.

Chatrou, L. W. & Pirie, M. D. 2005. Three new rarely collected or endangered species of Annonaceae from Venezuela. *Blumea* 50: 33-40.

Chatrou, L. W., Rainer, H. & Maas, P. J. M. 2004. Annonaceae. In: N. Smith, S.A. Mori, A. Henderson, D.W. Stevenson & S.V. Heald (eds.), Flowering Plants of the Neotropics: 18-20. Princeton University Press, New Jersey.

Erkens, R. H. J., Chatrou, L. W., Maas, J. W. & Savolainen, V. (chapter 4, this thesis). A major radiation of rainforest trees from Central into South America.

Fries, R. E. 1939. Revision der Arten einiger Annonaceen-Gattungen V. *Acta Horti Berg.* 12: 289-577.

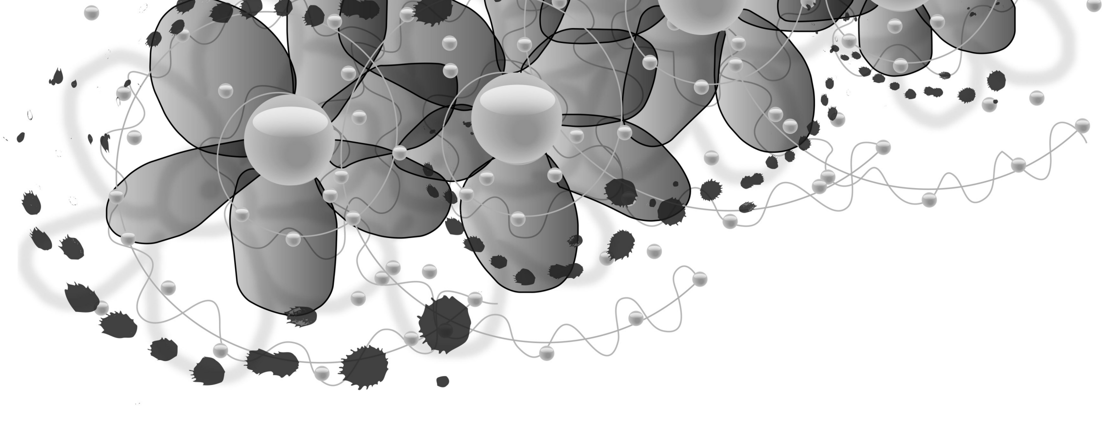
Ruiz Lopez, H. & Pavón, J. A. 1794. Florae peruvianae, et chilensis prodromus. Imprenta de Sancha, Madrid.

Scharf, U., Maas, P. J. M. & Morawetz, W. 2005. Five new species of Guatteria (Annonaceae) from the Pakaraima Mountains, Guyana. *Blumea* 50: 563-573.

Schatz, G.E. 1987. Systematic and ecological studies of Central American Annonaceae. PhD thesis, University of Wisconsin, Madison.

Weberling, F. & Hoppe, J. R. 1996. Comparative morphological evaluation of inflorescence characters in Annonaceae. In: W. Morawetz & H. Winkler (eds.), Reproductive morphology in Annonaceae. Biosystematics and Ecology Series, 10: 29-53. Austrian Academy of Sciences, Vienna.

Zamora V., N., Jiménez M., Q. & Poveda A., L. J. 2000. Árboles de Costa Rica, Vol. II. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.



10

PRELIMINARY FLORA MESOAMERICANA TREATMENT OF *GUATTERIA*

Roy H.J. Erkens, Paul J.M. Maas[1] & George E. Schatz[2]

ABSTRACT

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

To be submitted to Flora Mesoamericana

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INTRODUCTION

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

MATERIALS AND METHODS

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

GUATTERIA RUIZ & PAV.

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

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

KEY TO THE SPECIES

1. Flowers terminal.

2. Inflorescence many-flowered; pedicels 15-65 mm long; leaves 10-22 x 3-7 cm; petals 25-40 mm long. Mexico, Guatemala.......................**7. *G. anomala***

2. Flowers solitary; pedicels 6-12 mm long; leaves 5-8 x 2-3.5 cm; petals 7-9 mm long. Panama.......................**2. *G. acrantha***

1. Flowers axillary.

3. Young twigs densely covered with erect hairs.

4. Leaf base cordate.

5. Lower side of leaves covered with reddish brown, soft hairs, upper side glabrous except for a hairy midrib; pedicels 9-17 mm long; monocarps 50-75. Costa Rica ....**15. *G. pudica***

5. Both sides of leaves covered with rough hairs; pedicels 20-40 mm long; monocarps 10-15. Panama.......................**24. *G.* aff. *tomentosa***

4. Leaf base acute, obtuse, or attenuate.

6. Midrib raised on the upper side of the leaf; leaves narrowly oblong-elliptic. Panama, Costa Rica.......................**8. *G. chiriquiensis***

6. Midrib impressed to flat on the upper side of the leaf; leaves narrowly ovate to narrowly obovate.

7. Leaves verrucose.

8. Sepals 15-20 mm long; monocarps 20-30 mm long; stipes 2-3 mm long. Costa Rica, Panama.......................**22. *G. talamancana***

8. Sepals up to 10 mm long; monocarps up to 16 mm long; stipes 3-10 mm long.

9. Monocarp/stipes: 2.3-3; monocarps 9-16 mm long; stipes 3-7 mm long; young twigs often zigzagging. Costa Rica, Panama.......................**14. *G. oliviformis***

9. Monocarp/stipes: 1.2-1.6; monocarps 8-12 mm long; stipes 5-10 mm long; young twigs straight.

10. Petioles 1-5 x 2-4 mm; leaves 18-42 x 5-13 cm; petals 13-32 mm long. Nicaragua, Costa Rica, Panama.......................**3. *G. aeruginosa***

10. Petioles 3-9 x 1-2 mm; leaves 10-17 x 3-5 cm; petals 10-12 mm long. Panama.......................**26. *G. zamorae***

7. Leaves not verrucose.
11. Young twigs distinctly winged; flower buds distinctly pointed (see also ***G. recurvisepala***); petals brown to chocolate-coloured; leaves coriaceous. Panama........................**1. *G. aberrans***
11. Young twigs terete; flower buds rounded; petals green to yellow, sometimes brownish (in ***G. recurvisepala***); leaves chartaceous (sometimes coriaceous in ***G. recurvisepala***).
12. Sepals 2-5 mm long; petals canary yellow; leaves greenish when dried. Panama..**5. *G. allenii***
12. Sepals 5-13 mm long; petals green, brown to yellow (but never canary yellow); leaves never greenish when dried;
13. Sepals appressed to patent; upper side of leaves covered with erect hairs. Panama..**23. *G. tomentosa***
13. Sepals recurved; upper side of leaves glabrous except for the hairy midrib.
14. Leaves 11-14 x 3-5 cm; sepals 5-7 mm long; seeds pitted. Nicaragua to Panama..**10. *G. dolichopoda***
14. Leaves 15-32 x 5-13 cm; sepals 6-11 mm long; seeds smooth. Costa Rica, Panama...**16. *G. recurvisepala***

3. Young twigs covered with appressed hairs or glabrous.
15. Young twigs distinctly winged. Costa Rica, Panama..**4. *G. alata***
15. Young twigs terete.
16. Leaves mostly folded when dried. Panama..**11. *G. jefensis***
16. Leaves never folded when dried.
17. Leaves distinctly rounded at the apex, densely verrucose. Panama.......................**19. *G. rotundata***
17. Leaves acuminate or sometimes acute at the apex, sometimes verrucose.
18. Monocarps sessile or very shortly stipitate (stipes up to 3 mm long).
19. Leaves 18-33 x 5-10 cm, densely verrucose on the lower side. Panama..**20. *G. sessilicarpa***
19. Leaves 7-20 x 3-6 cm, not or sparsely verrucose on the lower side.
20. Monocarps globose, 20-25 mm diam.; pedicels 10-18 mm long. Costa Rica...**27. *G.* sp. 1**
20. Monocarps ellipsoid, 10-14 x 4-8 mm; pedicels 3-7 mm long. Costa Rica...**17. *G. reinaldii***

18. Monocarps distinctly stipitate with stipes >3 mm long.
21. Monocarps distinctly beaked at the apex; petiole 15-20 mm long. Costa Rica..**18. *G. rostrata***
21. Monocarps rounded to minutely apiculate at the apex; petiole mostly much shorter than 15 mm (but see under *G. slateri*).
22. Young stems mostly zigzagging; secondary veins raised on the upper side of the leaves.
23. Monocarps/stipes: 3.4-5; leaves verrucose.................**25. *G. verrucosa***
23. Monocarps/stipes: 0.7-2.6; leaves not verrucose.
24. Monocarp/stipes: 1.6-2.6; stipes 3-6 mm long; upper side of leaves glabrous. Panama...**21. *G. slateri***
24. Monocarp/stipes: 0.7-0.8; stipes 8-14 mm long; upper side of leaves with a hairy midrib. Costa Rica..........**9. *G. costaricensis***

22. Young stems straight; secondary veins impressed or raised on the upper side of the leaves.
25. Secondary veins raised.
26. Basal margins revolute; monocarps 40-75; seeds slightly pitted. Costa Rica, Panama.........................**13. *G. lucens***
26. Basal margins not revolute; monocarps 10-20; seeds brain-like. Mexico...**12. *G. galeottiana***
25. Secondary veins impressed.
27. Pedicels 35-50 mm long; sepals 4-5 mm long. Panama...**28. *G.* sp. 2**
27. Pedicels 10-35 mm long; sepals 3-12 mm long. Throughout Central America.............................**6. *G. amplifolia***

DESCRIPTIONS OF SPECIES OF GUATTERIA

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

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

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

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

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

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

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

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

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

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

Trees 5-20 m. Young twigs densely covered with erect, brown hairs. Leaves 18-42 x 5-13 cm, narrowly oblong-elliptic to narrowly obovate, chartaceous, densely verrucose, sparsely covered with appressed hairs above, but midrib densely covered with erect, brown hairs, densely to sparsely covered with erect, brown hairs below; base acute to obtuse, often slightly derurrent into the petiole; apex acuminate (acumen 10-20 mm long); midrib flat to impressed above; secondary veins distinct, 12-24 per side, flat to prominent above. Petioles
1-5 x 2-4 mm. Flowers solitary; pedicels 13-30 mm, densely covered with erect, brown hairs. Sepals 4-10{-16} x 5-9{-14} mm, broadly ovate-triangular, appressed, later becoming reflexed, outer side densely covered with appressed and erect, brown hairs. Petals yellowish green to creamy yellow, subequal, ovate-oblong to ovate-trullate, 13-32{-35} x 6-22{-27} mm, outer side densely covered with appressed and erect, brown hairs. Stamens 1.5-2 mm, connective shield densely papillate to hairy. Carpels ca. 50. Monocarps 20-50, green, maturing purple-black, 8-12{-15} x 4-6{-9} mm, ellipsoid, subglabrous, apex apiculate, stipes 5-10 mm. Seed 8-10 x 4-5 mm, ellipsoid, brain-like. *Forest.* N (*Rueda & al. 5796*, MO); CR (*Maas & al. 9427*, U); P (*Gordon 5*, MO). 0-1200 m. (Endemic).

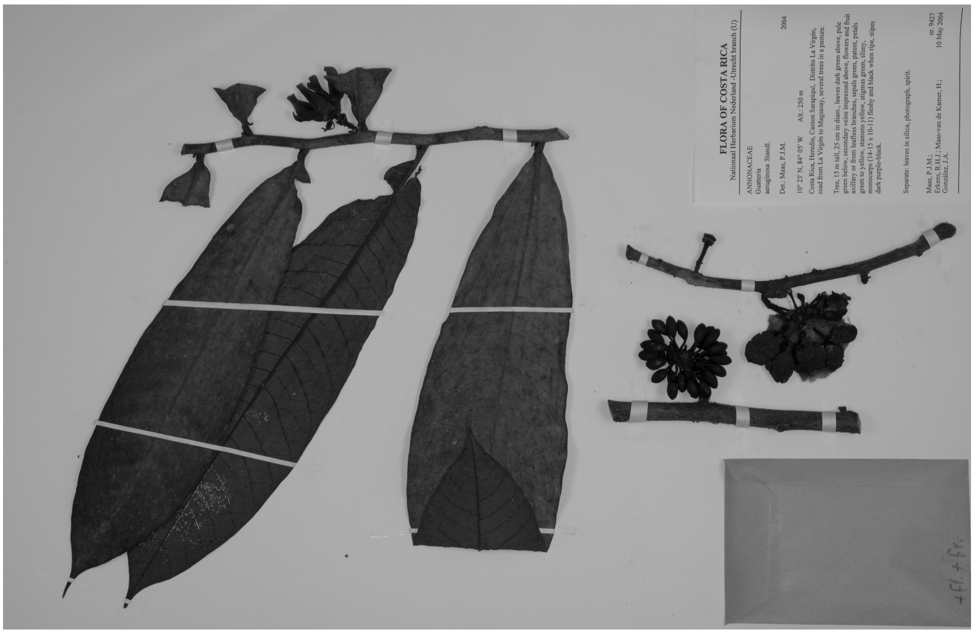
Guatteria aeruginosa is typical by its dense indument of erect, brown hairs and its densely verrucose leaves. The basal part of the pedicels is often provided with 2-3 remnants of bracts. The material from Nicaragua, the Heredia region in Costa Rica and the Bocas del Toro region in Pamana is less verrucose,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

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

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

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

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



Top: *Guatteria aeruginosa* Standl. (*Maas 9427*, U).

Bottom: *Guatteria alata* Maas & Setten (*McPherson 13675*, U).

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

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

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

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

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

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

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

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

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

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

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

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

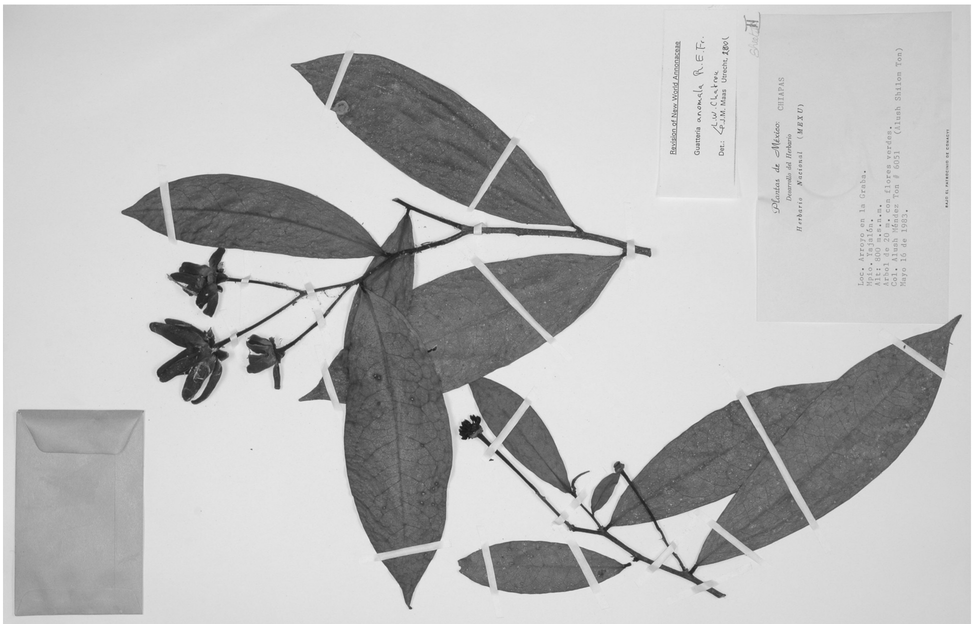
7. Guatteria anomala R.E. Fr., *Acta Horti Berg.* 12(3): 524. t. 1a-f (1939). Holotype: Guatemala, *von Tuerckheim 7816* (B).

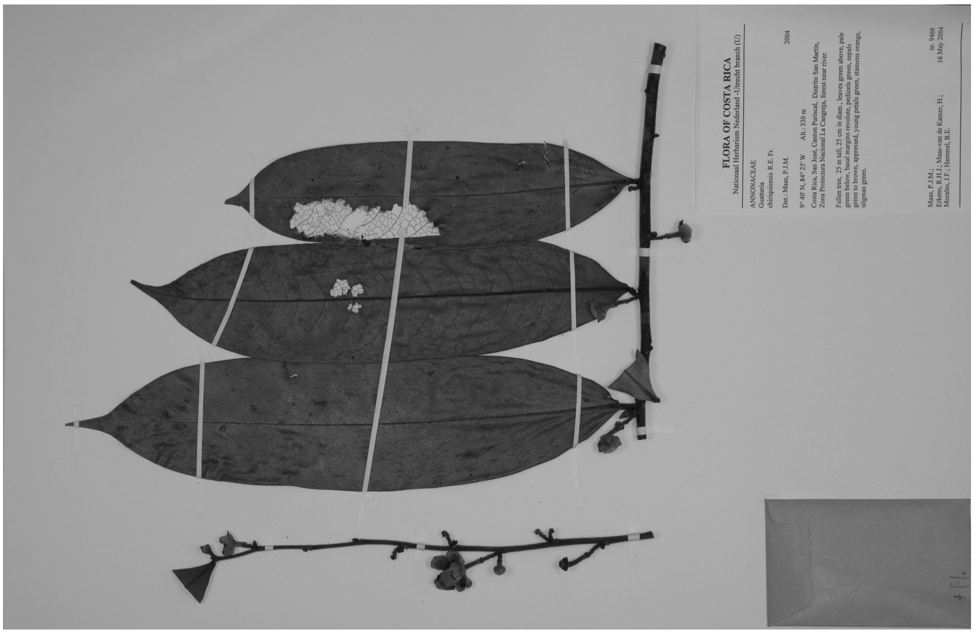
Trees 10-60 m, with deeply fluted stems. Young twigs rather densely covered with appressed, white hairs, very soon glabrous. Leaves 10-22 x 3-7 cm, narrowly obovate to narrowly elliptic, chartaceous, not verrucose, glabrous above and below; base acute, attenuate; apex shortly acuminate (acumen 2-10 mm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

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

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

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





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

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

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

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

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

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

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

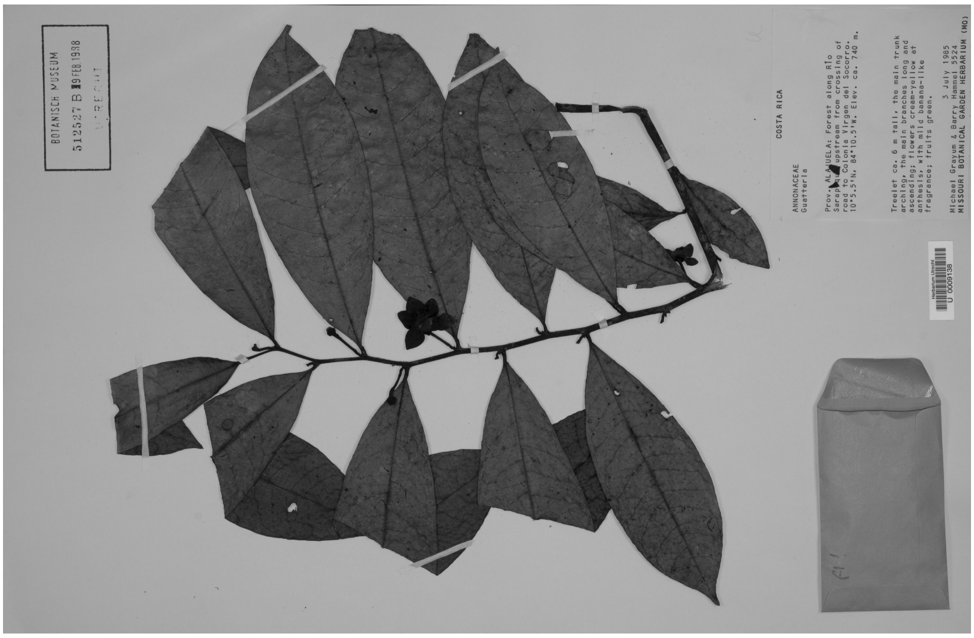
Guatteria costaricensis has often been confused with *G. oliviformis,* but is aberrant by its non-verrucose leaves, its indument of appressed hairs on its young twigs, its longer stipes, its smaller sepals and seeds and its greyish or brownish black leaves after drying.

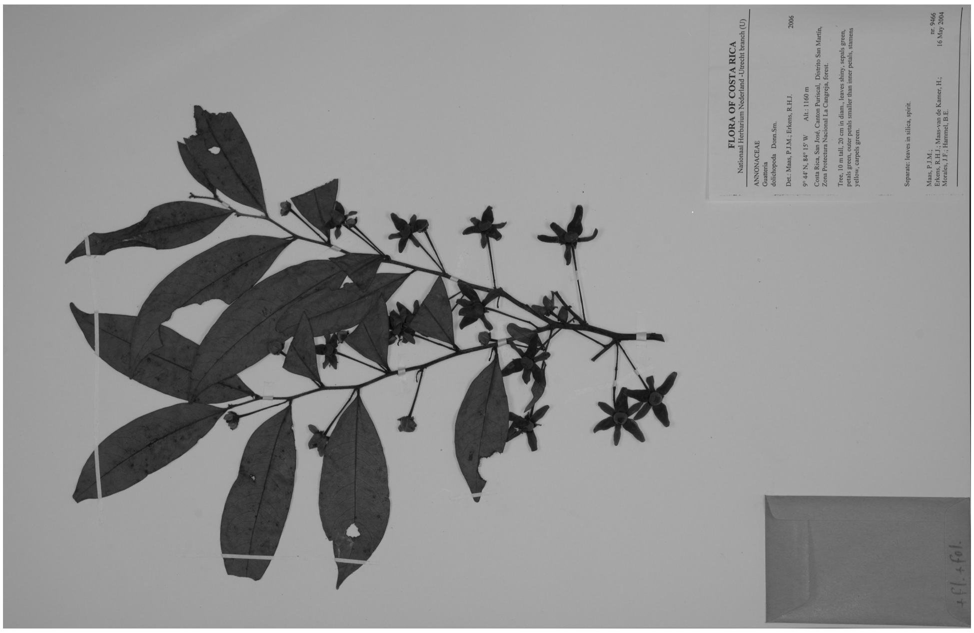
The Panamanian material of *G. costaricensis* seems to resemble the small leaved material of *G. slateri*. For the differences with *G. slateri* see under that species.

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

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

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





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

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

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

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

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

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

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

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

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

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

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

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

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

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

Guatteria dumetorum R.E. Fr.

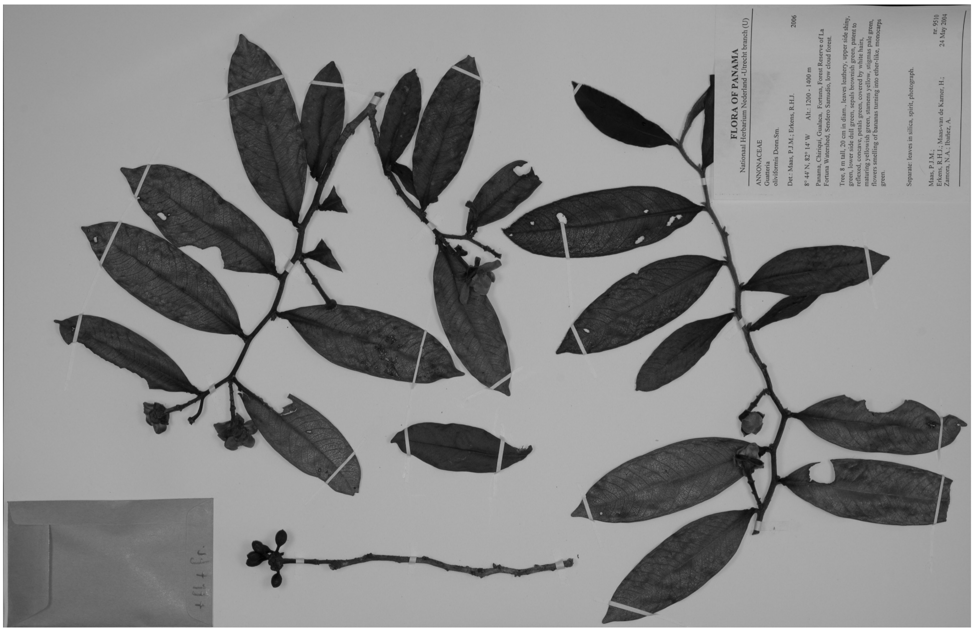
Trees 8-38 m. Young twigs densely to sparsely covered with appressed hairs, soon glabrous. Leaves 10-21 x 2-6 cm, narrowly elliptic to narrowly obovate, chartaceous, densely or not verrucose, shiny above, glabrous above, sparsely, sometimes rather densely covered with appressed hairs below; base long-attenuate,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

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

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

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

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



Top: *Guatteria lucens* Standl. (*Maas 9486*, U).

Bottom: *Guatteria oliviformis* Donn. Sm. (*Maas 9510*, U).

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

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

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

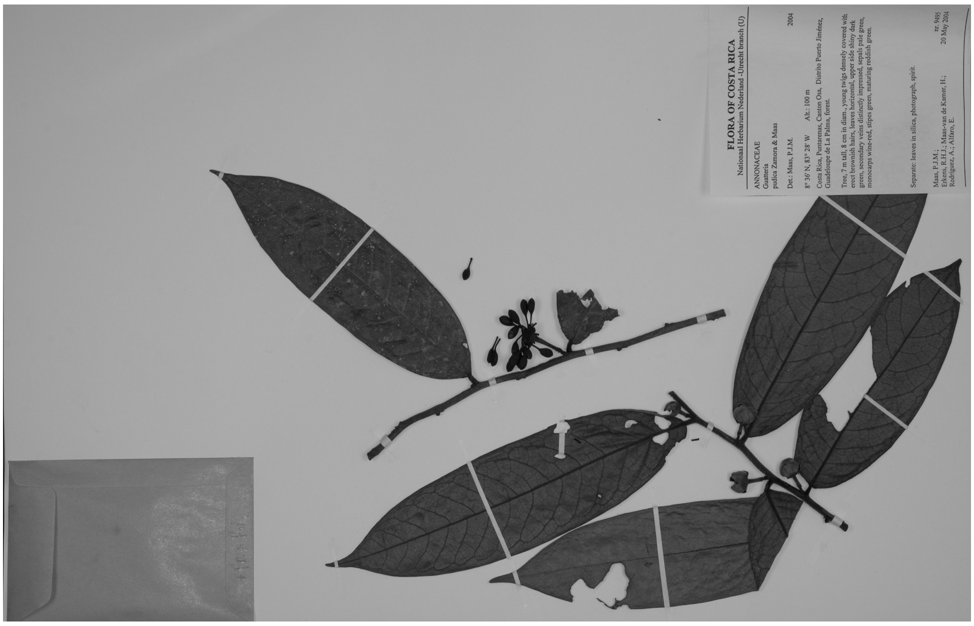
15. Guatteria pudica N. Zamora & Maas, *Bot. Jahrb. Syst.* 122: 244. f. 3-5 (2000). Holotype: Costa Rica, *Herrera 4026* (INB).

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

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

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

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



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

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

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

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

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

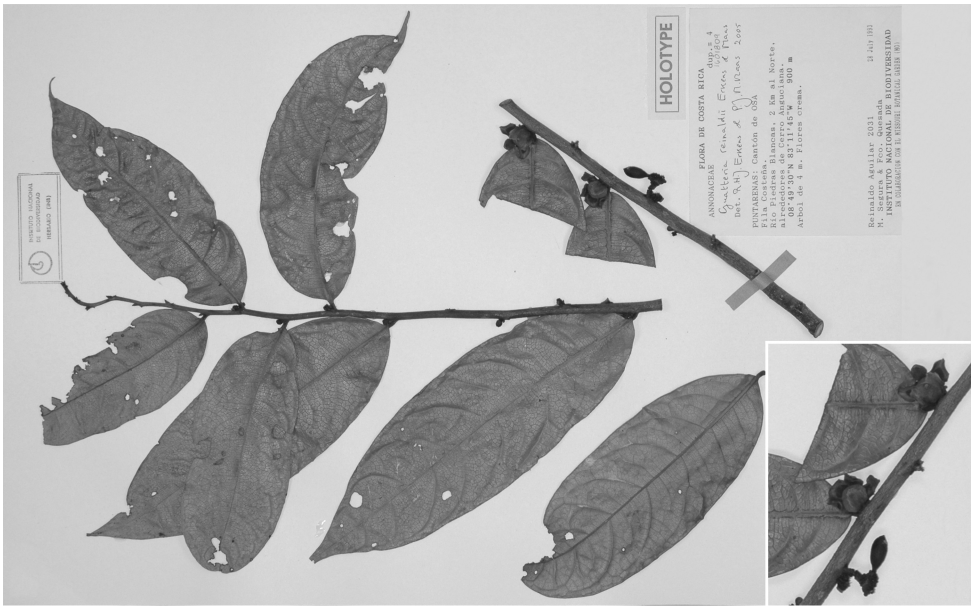
Trees 4-10 m. Young twigs rather densely covered with appressed hairs, soon glabrous. Leaves 13-20 x 4-6 cm, narrowly ovate to narrowly elliptic, chartaceous, sparsely or not verrucose above, shiny above, glabrous above, except for some hairs along primary vein, sparsely to rather densely covered with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

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

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

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

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



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

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

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

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

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

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

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

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

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

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

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

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

Herbarium Utrecht
U 0011390

ANNONACEAE
PANAMA
Prov. Panamá: Near continental divide. Valley of Río Mamoni, 10 miles by road N of Chepo, c. 9°20'N, 79°08'W. Forested slopes c. 400 m.
Tree 12 m; perianth green to yellow.
Gordon McPherson 8475 21 Feb. 1986
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Revision of New World Annonaceae
Guatteria rotundata P. Maas & van Setten
Det.: P.J.M. Maas
A.K. van Setten
Utrecht 1987

FLORA OF PANAMA
Nationaal Herbarium Nederland -Utrecht branch (U)
ANNONACEAE
Guatteria
sessilicarpa Maas & van Setten
Det.: Maas, P.J.M. 2004
9° 13' N, 79° 21' W Alt.: 750 m
Panama, Panama, near Cerro Jefe, Alto de Pacora, in pasture near road.
Tree, 8 m tall, 20 cm in diam., leaves coriaceous, upper side dull green, lower side dull paler green, basal margins revolute, sepals slightly reflexed, green with brown hairs, petals yellowish green, maturing yellow, stamens yellow, stigmas green, fruit green, maturing black.
Separate: leaves in silica, photograph, spirit.
Maas, P.J.M.; nr. 9554
Erkens, R.H.J.; Maas-van de Kamer, H.; 6 June 2004
Zamora, N.A.; Aizprúa, R.

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

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

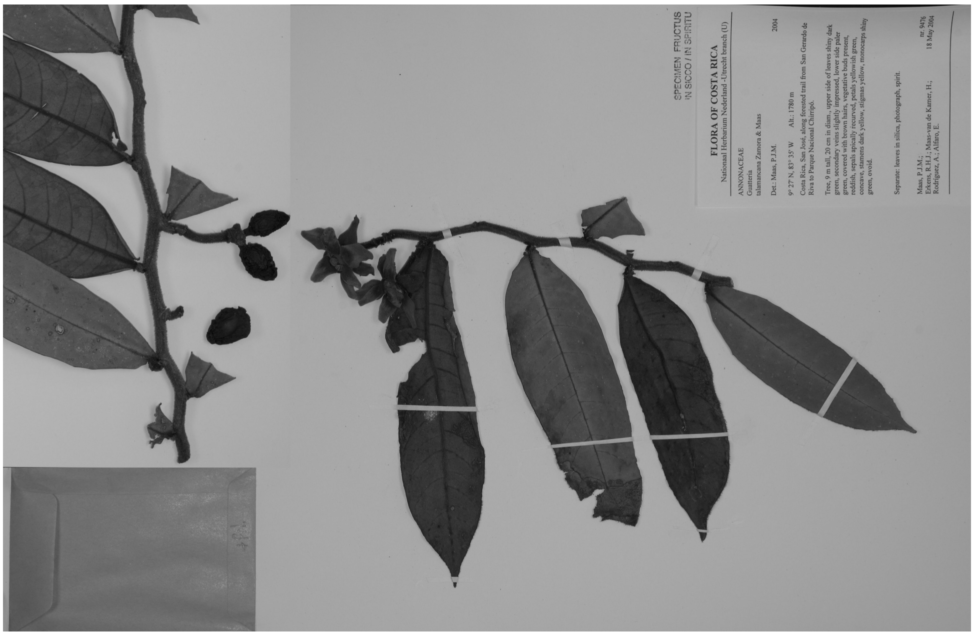
narrowly obovate, chartaceous to coriaceous, not verrucose, glabrous above, sparsely covered with appressed, brown hairs to glabrous below; base acute to attenuate; apex acuminate (acumen 5-15 mm long); midrib slightly raised to flat above, often keeled below; secondary veins distinct, 8-15(-20) per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

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

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

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

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



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

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

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

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

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

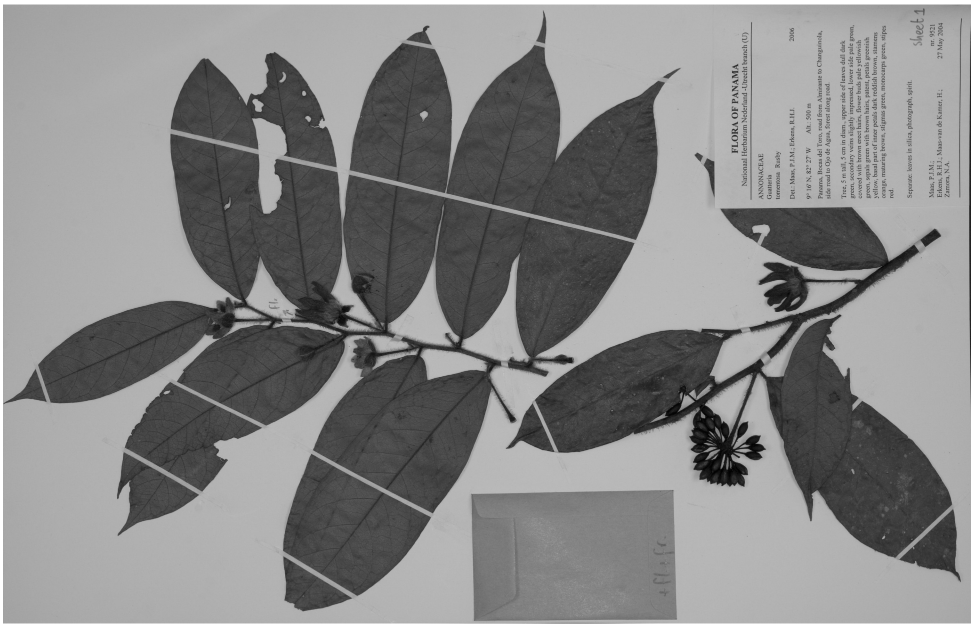
We have tentatively named this species *Guatteria tomentosa,* a species which is widespread over Central America and Western South America. It is a highly variable and complex species, including closely related species like *G. trichoclonia* Diels, which needs an intensive taxonomic study. It is easily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

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

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

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

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



FLORA OF PANAMA
Nationaal Herbarium Nederland -Utrecht branch (U)

ANNONACEAE
Guatteria
tomentosa Rusby

Det.: Maas, P.J.M.; Erkens, R.H.J. 2006

9° 16' N, 82° 27' W Alt.: 500 m

Panama, Bocas del Toro, road from Almirante to Changuinola, side road to Ojo de Agua, forest along road.

Tree, 5 m tall, 5 cm in diam., upper side of leaves dull dark green, secondary veins slightly impressed, lower side pale green, covered with brown erect hairs, flower buds pale yellowish green, sepals green with brown hairs, patent, petals greenish yellow, basal part of inner petals dark reddish brown, stamens orange, maturing brown, stigmas green, monocarps green, stipes red.

Separate: leaves in silica, photograph, spirit.

sheet 1

Maas, P.J.M.; nr. 9521
Erkens, R.H.J.; Maas-van de Kamer, H.; 27 May 2004
Zamora, N.A.

FLORA OF PANAMA
Nationaal Herbarium Nederland -Utrecht branch (U)

ANNONACEAE
Guatteria
aff. tomentosa

9° 14' N, 79° 21' W Alt.: 750 m

Panama, Panama, near Cerro Jefe, Alto de Pacora, 400 m before the ANAM office, forest along roadside.

Tree, 6 m tall, 7 cm in diam., leaves concave, upper side dull green, lower side paler dull green, basal margin revolute, sepals green, appressed, petals yellowish green, stamens dark yellow, stigmas green.

Separate: leaves in silica, spirit, photograph.

Maas, P.J.M.; nr. 9555
Erkens, R.H.J.; Maas-van de Kamer, H.; 6 June 2004
Zamora, N.A.; Aizprúa, R.

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

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

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

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

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

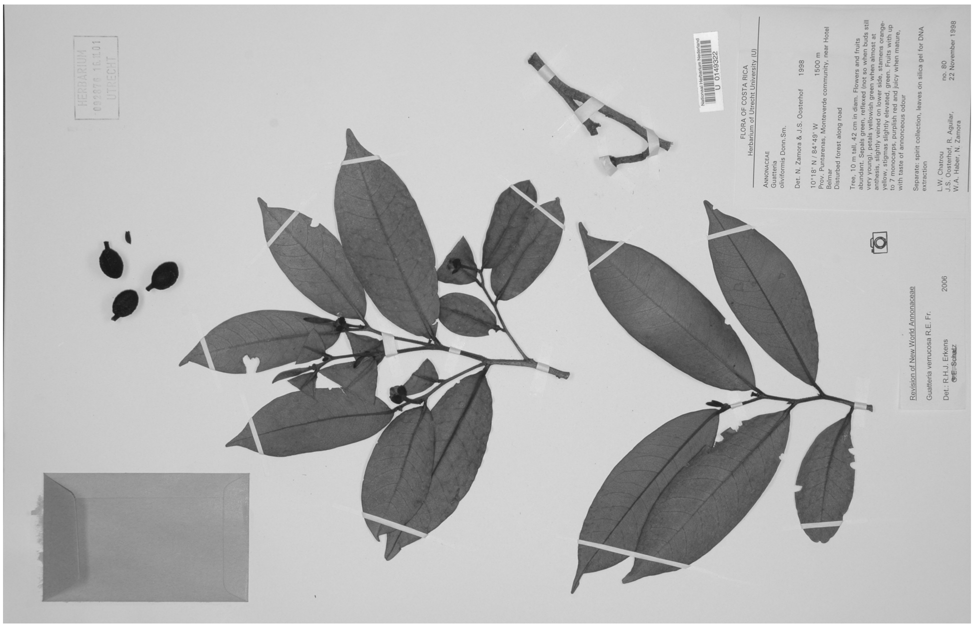
Trees 3-28 m. Young twigs rather densely covered with appressed hairs, to glabrous. Leaves 7-17 x 2.5-5 cm, narrowly elliptic to elliptic, chartaceous, verrucose above and below, dull, glabrous above, sparsely covered with minute appressed hairs below; base acute to attenuate, decurrent along the petiole;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

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

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

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

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



FLORA OF COSTA RICA
Herbarium of Utrecht University (U)

ANNONACEAE
Guatteria
oliviformis Donn.Sm.

Det. N. Zamora & J.S. Oosterhof 1998

10°18' N / 84°49' W 1500 m
Prov. Puntarenas, Monteverde community, near Hotel Belmar
Disturbed forest along road

Tree, 10 m tall, 42 cm in diam. Flowers and fruits abundant. Sepals green, reflexed (not so when buds still very young), petals yellowish green when almost at anthesis, slightly veined on lower side, stamens orange-yellow, stigmas slightly elevated, green. Fruits with up to 7 monocarps, purplish red and juicy when mature, with taste of annonceous odour

Separate: spirit collection, leaves on silica gel for DNA extraction

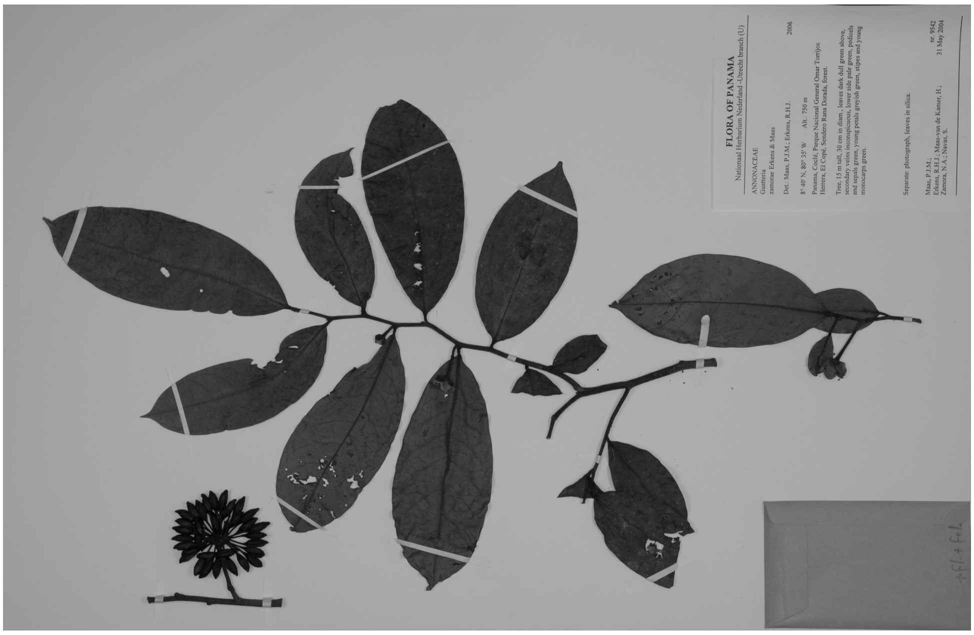
L.W. Chatrou no. 80
J.S. Oosterhof, R. Aguilar, 22 November 1998
W.A. Haber, N. Zamora

U 01449322

Revision of New World Annonaceae

Guatteria verrucosa R.E. Fr.

Det.: R.H.J. Erkens 2006
~~G.E. Schatz~~



FLORA OF PANAMA
Nationaal Herbarium Nederland -Utrecht branch (U)

ANNONACEAE
Guatteria
zamorae Erkens & Maas

Det.: Maas, P.J.M.; Erkens, R.H.J. 2006

8° 40' N, 80° 35' W Alt.: 750 m

Panama, Coclé, Parque Nacional General Omar Torrijos Herrera, El Copé, Sendero Rana Dorada, forest.

Tree, 15 m tall, 30 cm in diam., leaves dark dull green above, secondary veins inconspicuous, lower side pale green, pedicels and sepals green, young petals greyish green, stipes and young monocarps green.

Separate: photograph, leaves in silica.

Maas, P.J.M.; nr. 9542
Erkens, R.H.J.; Maas-van de Kamer, H.; 31 May 2004
Zamora, N.A.; Navas, S.

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

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

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

27. Guatteria sp. 1

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

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

28. Guatteria sp. 2

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

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

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

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

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

INSUFFICIENTLY KNOWN SPECIES

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Guerra, C. 1085 (sp.)
Gustafson, C. 191 (amp)

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

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

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

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

Khan, T. 728 (amp); 1128 (cos); 1285 (oli)
Kinloch, J.B. 63 (amp)
Kirkbride, J.H. 581 (tom); 1037 (sp.); 1453 (sp2)
Knapp, S. 1077 (all); 2049 (sla); 2556 (sp.); 3554 (jef); 4497 (dol); 4580 (jef); 4984 (cos); 5853 (amp)
Knight, D. s.n. (amp)
Koptur, S. 113 (ver)
Kress, W.J. 94-4900 (dol)
Kriebel, R. 183, 434 (amp)

Laguna, A. 141 (amp)
Lankester, C.H. 138 (oli); 1925 (amp)
Lao, E.A. 96 (aer); 570 (rec)
Laskowski, C. 1299 (rec)
Lawton, R.O. 1145 (ver)
Lellinger, D.B. 1280 (ver)
Lems, K. 5154 (oli); 5165 (rec)
Lent, R.W. 1622 (oli); 2244 (amp); 2383 (sp.); 2527 (amp); 2619 (cos); 2902 (amp); 3000, 3032 (oli); 3145 (sp.); 3330 (amp); 3460, 3764 (oli)
Léon, J. 792 (dol)
Lewis, W.H. 1996 (tom)
Lezama, D. 104 (amp)
Liebmann, F.M. 12 (amp, Type); 14 (amp?); 143 (gal)
Liesner, R.L. 700, 3171 (amp); 4380 (all); 14631 (amp); 14981 (cos); 15199, 15361 (amp); 15579 (ver); 26145 (amp)
Little Jr., E.L. 25246 (amp)
Lobo, M.G.A. 114 (amp)
Long, L.E. 136 (amp)
Lorener, D.H. 4061 (amp)
Lot, A. 2230 (amp)
Luque, D. 509, 566 (abe)
Luteyn, J.L. 578, 583 (oli); 1230 (all)

Maas, P.J.M. 1127, 1590, 7805 (amp); 7817, 7822 (rec); 7869 (pud); 7926, 7964 (amp); 7966 (cos); 7973 (dol); 8001 (oli); 8492 (amp); 8496 (tom); 9392, 9399 (cos); 9417 (amp); 9418 (aer); 9419 (amp); 9427 (aer); 9432 (rec); 9448 (amp); 9462 (dol); 9464 (chi); 9465, 9466 (dol); 9469 (chi); 9471 (oli); 9476 (tal); 9479 (sp.); 9483 (rec); 9484 (tom); 9486, 9491, 9492 (luc); 9493 (ros); 9495, 9496 (pud); 9497 (ros); 9498 (amp); 9508, 9509 (dol); 9510 (oli); 9513 (sla); 9516 (tal); 9519 (luc); 9521 (tom); 9523 (luc); 9525 (sp.); 9528 (tom); 9531 (zam); 9533, 9534 (amp); 9538 (all); 9539 (amp); 9542 (zam); 9543 (all); 9545 (sp.); 9549 (amp); 9553 (jef); 9554 (ses); 9555 (tom aff); 9556, 9561 (sp.); 9562 (rec); 9564, 9570 (abe); 9574 (amp); 9581 (luc)
Manriquez, G.I. 2346 (amp)
Marín, J. 45 (ros); 236 (amp)
Marshall, N.T 336 (amp)
Martén, S. 748 (amp); 1075 (aer)
Martinez, M. 31 (amp)
Martínez S., E.M. 17675, 18627 (ano); 23614 (amp); 25429 (amp)
Matuda, E. 3685 (amp)
McDade, L.A. 807 (amp)
McDaniel, S. 10242 (sp.)
McDowell, T. 777 (amp); 818 (aer); 1003 (amp)
McPherson, G. 6805 (sla); 6879 (jef); 6958, 6959 (amp); 7116 (jef); 7204 (sla); 7466 (ses); 7485, 7595 (amp); 7705, 7816 (sla); 7844, 7870 (tal); 7992 (amp); 7995 (ala); 8027, 8028 (sla); 8114 (luc); 8295 (sla); 8463 (amp); 8475 (rot); 8497 (ses); 8676, 8722 (tom); 8781 (sla); 8851 (oli); 8866, 8944 (sla); 9123 (tom); 9138, 9583 (sla); 9944 (ses); 10177 (amp); 10187 (tom); 10230 (amp); 10317 (rec); 10354 (luc); 10398 (sp.); 10478 (dol); 10739 (sla); 10941 (rec); 11118 (sla); 11200, 11262 (all); 11287 (ses); 11313 (sla); 11481 (amp); 11596 (sp2); 11756, 11869, 11898 (amp); 12084 (sla); 12143 (all); 12222, 12227 (sp2); 12599 (ses); 12689 (sla); 12787, 12812 (sp2); 13646 (sla); 13658 (tom); 13675 (ala); 14075 (sp2); 15405 (rec)
Meave, J. 1097, 1372 (amp)
Méndez, P. Ton, A. 6051, 6511 (ano)
Méndez, R. 114, 147 (sp2)
Miller, J.S. 841, 944 (amp)
Molina R., A. 1844, 1857 (amp); 2011 (rec); 13453, 17217 (amp); 17467 (dol); 18022, 18226, 18324 (rec); 25634 (dol)
Monro, A.K. 2634, 4257 (amp); 4453, 4924 (sp.); 4925 (tal); 5051 (sp.)
Montenegro, E. 1174 (sla); 1948 (tom aff)
Mora, E. 577 (luc); 583, 668, 1146, 1748 (amp); 1924 (ver)
Mora, G. 12, 276 (dol); 413 (oli)
Moraga, C. 45 (aer); 719, 822 (amp)
Moraga, M. 262 (amp)
Morales, C. 24 (amp)
Morales, J.F. 27 (dol); 367 (tal); 388 (oli); 480, 2024 (dol); 2456 (ver); 2726 (oli); 4237 (oli) ; 6426 (chi); 7567 (sp.); 7731 (amp)
Moreno, A. 27 (amp); 70 (sp.)
Moreno, P.P. 12011, 12015, 12169, 12210, 12319, 12471, 12616, 13035, 13038, 13166, 13178, 13260, 14578, 14752, 14779, 23084, 23875B, 23934, 24118, 24638, 24956, 25577 (amp); 26097 (tom); 26257, 29954 (amp)
Mori, S.A. 2315 (luc); 2894 (ala); 2952, 2980 (all); 3046 (amp); 3319 (ses); 3324 (amp); 4246 (sp2); 4555 (amp); 4981 (ses); 5037 (ses, Type); 5283 (sp.); 5494 (tom); 5531 (rot); 6078 (jef); 6256 (dol)6410 (all); 6501 (jef) ; 6542 (tom aff); 6612 (all); 7978 (amp)
Murray, N.A. 816 (rec); 1384 (amp); 1478 (all); 1483 (tom)

Navarro V., E. 263 (dol); 697 (dol)
Nee, M. 7099, 7930, 8715, 9092 (amp); 9147 (sp.); 9290 (amp); 10999 (rot, Type); 11078 (amp); 11277 (tom); 18818, 19990, 22717, 22721 (gal); 24723, 25079 (amp); 29819, 29949 (gal)
Neill, D. 2606, 4364, 5041 (amp)
Nelson, C. 850, 2681, 3282; 4765 (amp)
Nelson, E.B. 4189 (amp)
Nevers, G. de 4055 (sp.); 4303 (rot); 4473, 4822 (amp); 4986 (sp.); 4993 (amp); 5258 (rot); 5387 (sp.); 5564, 6110, 6423, 6603 (amp); 6873 (rec); 6923, 6968 (amp); 7168 (abe); 7540 (abe); 7578 (sp.); 8388, 8425 (sp2)
Nevling, L.I. 2598 (amp)

Opler, P.A. 424 (sp.); 807 (amp)
Orozco, A.D.L. 332 (amp)
Ørsted, A.S. 146 (cos, Type)
Ortega O., R. 1173 (gal)
Ortiz, B. 160 (gal)
Ortíz, R.T. 2330, 2332 (amp)
Ortíz C., D. 886 (gal)

Paredes, R. 790 (amp); 954 (sp.)
Penneys, D. 406 (cos)
Pennington, T.D. 9612 (ano); 11525 (aer)
Pérez, R. 550 (amp); 863 (luc); 882 (abe); 1028 (ses)
Perino, C.H. 3186 (gal)
Peterson, P.M. 6612, 6758 (tom); 6814, 7195, 8665 (amp)
Picado, A. 83 (dol)
Pipoly, J.J. 7042 (jef)
Pittier, H. 3915 (luc, Type); 10958 (dol, Type); 16015 (amp)
Ponce C., F. 19 (gal)
Poveda, L.J. 62 (dol); 698 (amp); 3911 (chi)
Proctor, G.R. 27116 (rec)

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

Rainer, H. 151 (amp); 157 (chi); 158 (amp)
Ramírez, V. 73 (amp); 354 (amp)
Ríos, D.E. 169 (amp)
Ríos, P. 37, 85 (amp)
Riveira, N. 355 (acr); 948 (dol); 1390 (dol)
Rivera, G. 539 (dol); 1000 (amp); 1069 (cos); 1390 (dol); 1693 (sp.); 1727 (dol); 2041 (oli)
Rivière, R. 359 (amp)
Robinson, B.L. 50 (amp)
Robles, R. 1243, 1284, 1326, 1930 (amp); 2042, 2068 (rec); 2109 (amp); 2828 (aer)
Robleto, W. 645 (amp)
Robyns, A. 65-31 (amp)
Rodríguez, A. 687 (luc); 1080 (oli); 1408 (aer); 2194 (dol); 2213 (amp); 3581 (ver); 4322 (luc); 4567, 5189 (amp); 5195 (aer); 7083 (amp); 7185 (dol); 7254 (cos)
Rodríguez, G. 17 (cos)
Rojas, E. 89 (chi); 143 (amp)
Rueda, R. 1486, 1666, 2587, 2645, 3498, 4100, 4104, 4136 (amp); 4137, 4871 (aer); 4930 (tom); 5444 (amp); 5796 (aer); 8545, 8635 (amp); 8730 (aer); 9637, 9659 (amp); 9714 (aer); 9798, 9866, 9968 (amp); 10116, 10233 (aer)

Saborio, J.C. 79 (amp)
Sakai, S. 506 (luc)
San Emeterio, L. 395 (amp)
Sánchez, P. 501 (amp); 537 (cos)
Sandino, J.C. 1647, 3443, 4577, 4601, 4771, 5144 (amp)
Santamaría, D. 888 (sp.); 1022 (amp); 1109 (oli)
Saunders, J. 1192 (amp)
Shattuck, O.E. 634, 1095 (luc)
Schatz, G.E. 571, 650 (aer); 957 (rec); 991 (amp); 1097 (dol); 1212 (ros); 1214, 1216 (pud); 1217 (amp); 1218 (chi)
Schipp, W.A. 298, 406 (amp)
Schmalzel, R.J. 1593 (oli)
Schultes, R.E. 560 (gal)
Segura, M. 72 (chi); 155 (amp)
Sessé, M. de 2312, 2322 (amp)
Seymour, F.C. 3396, 3780 (amp)
Shank, P. 14167, 14168 (rec)
Shattuck, O.E. 406 (amp)
Skutch, A.F. 1800 (amp); 2553 (tom, Type); 2589 (rec); 3316, 3430 (oli); 4171 (tom); 4234 (rec, Type); 5078 (rec); 5323 (amp)
Smith, A. s.n. (July 15, 1937), 100, H221, H492, H883 (oli); F1824 (amp); P2532 (dol); 4230 (oli)
Smith, D. 343 (amp)
Solano, J. 6, 109 (amp)
Solís 4354 (amp)
Somoza, A. 111, 112 (sp.)
Soza, D. 5, 376 (amp)
Spellman, D. 187 (amp)
Sperry, J. 687 (amp)
Standley, P.C. 19354, 19973, 30272 (amp); 37132 (amp, Type); 52628, 54647, 73061 (amp)
Starry, D.E. 170, 325 (amp)
Steiner, K. 314 (amp)
Stern, W.L. 425, 527, 665 (sp2)
Stevens, W.D. 4875, 4946, 7576, 7633, 8851, 9003, 12476 (amp); 13348 (aer); 13500, 19785 (amp); 19831 (rec); 20078, 20657 (amp); 23641 (aer); 23801 (amp); 23899 (aer); 24084 (amp); 24906 (aer); 24510 (amp); 24542 (aer); 24783 (amp); 24812 (sp.); 24919, 24996, 25236, 25252 (amp)
Steyermark, J.A. 38691, 39813, 3988, 44220, 45115 (amp); 49410 (ano)
Stolze, R.G. 1557 (oli)
Stone, D.E. 3260 (oli); 2148 (amp)
Stork, H.E. 1048 (oli); 2598 (ten, Type)
Sucre, D. 4760 (amp)
Sullivan, G.A. 196 (tom aff); 210, 230 (jef)
Sytsma, K.J. 1476 (jef); 1953 (amp); 2692 (sp.); 2845 (jef); 2864, 3097, 4025 (amp); 4169 (rec); 4256, 4389 (amp); 4864 (sla)

Téllez V., O. 8523 (amp)
Tenorio L., P. 5250 (amp)
Thien, L.B. s.n. (March 1973) (amp); 4290 (jef)
Thomsen, K. 17, 24 (amp); 121 (luc); 142, 447, 575 (amp); 742 (pud); 941 (pud); 1193 (amp); 1232 (rec); 1469 (aer)
Tonduz, A. 9166 (dol, Type); 12970 (dol); 17680 (dol, Type)
Torres C., R. 81, 4485, 11157 (amp)
Türckheim, H. von 1480, 7815 (amp)
Tyson, E.L. 3424, 3593, 4348 (jef)

Utley, J.F. 927 (oli); 1245 (amp); 2141 (oli); 2439 (ver); 2608, 2755 (oli); 2844 (sp.); 3044 (oli); 3255a (sp.); 4935 (chi); 4954 (rec)
Utley, K. 6052 (amp)

Valdespino, I.A. 112, 286 (amp); 674, 682, 685 (jef)
Valerio, M. 74 (amp); 1015 (oli); 1281 (dol); 1647 (oli)
Valerio R., J. 1396 (oli)
Valverde, O. 258 (cos); 1039 (sp.); 1219, 1275 (amp)
Vargas, O. 218 (aer)
Vera Caletti, P. 109, 161 (gal); 170 (ano); 225 (amp)
Villarreal, D. 984 (sp2)
Villegas H., A. 128 (amp)

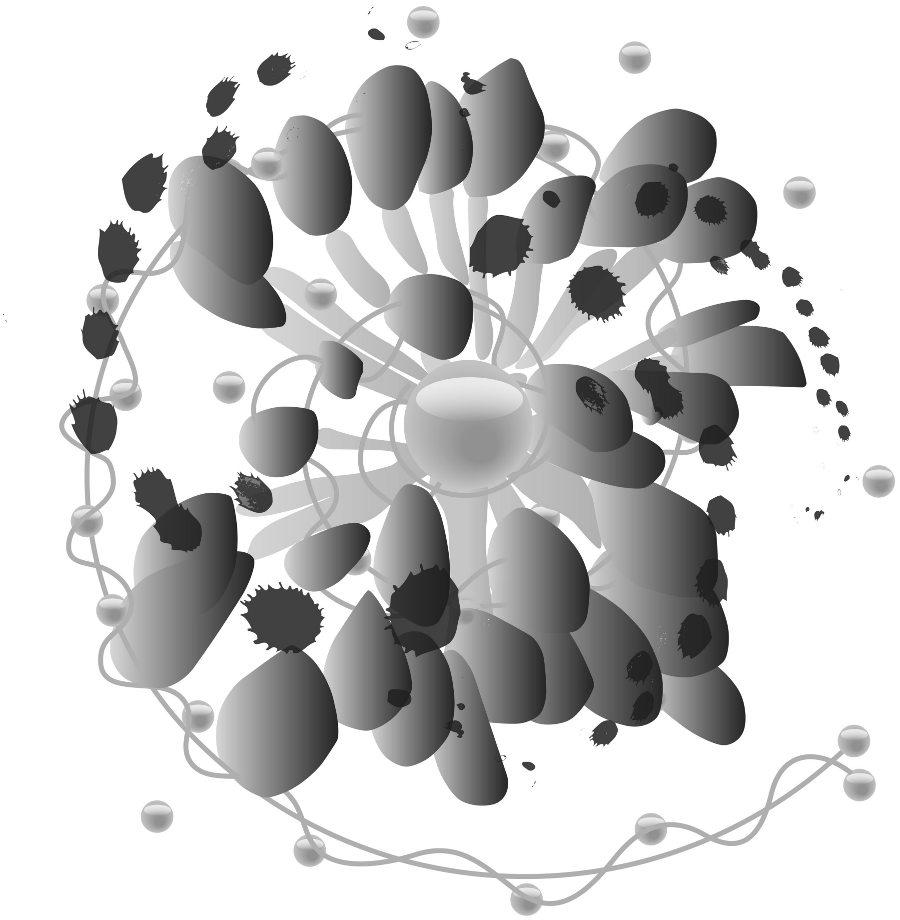
Walker, J.W. 118 (amp); 119 (aer); 194 (amp); 197 (chi); 205 (rec); 356, 361, 362, 363, 367 (amp); 383, 398 (tom); 413, 419 (oli)
Warszewicz, J. von 4 (oli)
Weaver, R.E. 1576 (luc)
Webster, G.L. 22054 (luc)
Wedel, H. von 155, 490 (aer); 907 (tom); 1460, 1716, 1932 (amp); 1965 (pan); 2108 (amp); 2856 (aer)
Wendt, T. 2831 (amp); 3057, 3303 (gal); 3330 (ano); 3572 (gal); 3755, 4268, 5672, 5677, 5692 (amp)
Werff, H. van der 6198, 6933 (sp2); 6964 (jef)
Whitefoord, C. 9332, 9337, 9373 (amp)
Wilbur, R.L. 9857, 10172 (oli); 10226 (dol);10846 (rec); 11005 (dol)
Williams, Ll. 9162, 9315 (amp)
Williams, L.O. 24244, 28718 (rec); 28737 (amp)
Williams-Linera, G. 145, 332 (amp);
Wilson, R.G. s.n. (28 Feb. 1964) (dol)

Yuncker, T.G. 6155 (ano)

Zamora, N. 774 (dol); 1253 (chi); 1320 (ver); 1461 (chi); 1468 (oli); 1655 (rec); 1735 (aer); 1811 (amp); 2100 (oli); 2268 (aer); 2270 (oli); 2313 (amp)
Zetek, J. 4629 (amp)
Zumbado, M. 76 (amp)
Zúñiga, R. 201, 528 (chi); 623 (dol)

LIST OF ABBREVIATIONS USED

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



11 VERNACULAR NAMES OF *GUATTERIA* (ANNONACEAE)

Roy H.J. Erkens & Erik A. Mennega†

ABSTRACT

Vernacular names of 73 out of c. 290 species of *Guatteria* (Annonaceae) are indexed. Several widespread species of this large Neotropical genus are often encountered and much collected while others are only rarely found. Localization of almost all *Guatteria* species is therefore interesting because there is a large lack of collections and (ecological) information of many little known species in the genus. Vernacular names can be helpful in communicating with locals in order to elicit information about localities of plants from them. Furthermore, dissemination of this taxonomic information on a larger scale, can contribute to the build up of an easy accessible body of knowledge about *Guatteria*. This is important because the large size of the genus inhibits comprehensive systematic knowledge in one single person. Four indices are included in this publication: (1) an index of scientific plant names, (2) an index of vernacular plant names, (3) an index of scientific plant names per geographical area, and (4) an index of vernacular plant names per geographical area. Index (1) and (3) might be most useful for botanical specialists that want to look up local names, while index (2) and (4) are meant for non-botanists who are unfamiliar with Latin botanical names.

Keywords: scientific plant names, vernacular names, cross reference

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Manuscript in preparation

INTRODUCTION

When preparing a botanical expedition to a certain geographical region many data are collected about that region. Information on the specimens that have been collected there before, the topography of the region and the possibility of local collaboration are examples of this. Especially when researchers are not native to a certain region, it may be useful to find out if vernacular names for the plants under study are available for that region and if they have been cross-referenced to botanical (Linnaean) names. In most planning for expeditions, preparation is solely based on Linnaean taxonomy, but knowledgeable local people may have a large amount of information on the local flora on the basis of folk taxonomies. This knowledge is of particular importance when skilled biologists and taxonomists are a scarce resource in that particular region (Cunningham, 2001). Local field guides often do not have a specialistic, scientific training. This does not mean that they have no information on the flora growing in their region. It does mean that they communicate in a different way about this knowledge (i.e. they do not use the Linnaean binomial classification system). Therefore, vernacular names can be used to elicit information about localities of plants from these guides and thus enhance the success of finding the target plants. For example, species of the pan-tropical family of Annonaceae are in the Spanish speaking countries of the Neotropics often identified with the general name "yaya." Even when it is difficult to communicate with field guides, using this name often results in a response and the localization of one or another Annonaceae species. Especially in poorly known and undercollected regions, vernacular names may be an important additional source of information to locate specimens. For these regions, only few reference collections exist and the chance of finding a specific target plant without local help is small.

The purpose of this article is to disseminate knowledge of the vernacular names of one of the largest genera of Neotropical trees, *Guatteria* (Annonaceae). The genus consists of approximately 290 species and can be found in primary low land tropical rain forests from southern Mexico to southern Brazil. Most species of *Guatteria* are small treelets to medium-sized trees. Although some species occur as somewhat isolated individuals, others form dense undergrowth populations (Morawetz & Waha, 1985). As a result, several widespread *Guatteria* species are often encountered and much collected (such as *G. megalophylla* or *G. schomburgkiana*) while others are only rarely found. The localization of such rarely collected species of which no extensive record of collection sites exists, can only be done with the help of local guides who know the plants in the area. Vernacular names are often the only means of communicating with these local field guides and thus are particularly important if no other information is available (Wilkie & Saridan, 1999). The fact that some vernacular names do not have an one-on-one correspondence with scientific names (Savolainen & al., 1995; Wilkie & Saridan, 1999) or that one name can include different species, does not pose a problem in this case. Localization of almost all *Guatteria* species is interesting because there is a large lack of collections and (ecological) information of many little known species in the genus.

A second reason to disseminate this knowledge is that the large size of the genus inhibits comprehensive systematic knowledge. In the limited time available for research projects these days, learning about the phylogeny, taxonomy, anatomy, karyology, chemistry, the many nomenclatural changes, etc. of so many species is impossible. Therefore, it is important to build up an easy accessible body of knowledge (which in itself can take many years) on which successors can build. A good example of such knowledge dissemination is Annonbase (Maas & al., 1994; extended and data based by Rainer & Chatrou, 2006), an online database that contains up-to-date nomenclatoral information (o.a. including location of type specimens, synonyms and references to literature) of all species of Annonaceae. This list is therefore an invaluable tool for the non-Annonaceae specialist. This type of information dissemination is especially important in a time that taxonomy is not fashionable anymore. As a result of this trend, for *Guatteria* almost no specialists exist and almost no young taxonomists are trained (and if so only on a regional scale and not on a comprehensive, genus-wide scale). Making taxonomic information accessible on a larger scale (e.g. via publications or the internet) can contribute to the usage of this knowledge by people who otherwise would not have had access to it. Unfortunately, the above mentioned problems are not specific for *Guatteria* but hamper research in many large, and mega-large genera (the latter containing > 500 species; Frodin, 2004).

METHODOLOGY

When vernacular names are collected for ethnobotanical research, stringent rules should be applied in order to be able to trustworthy analyse the results obtained. For instance, the language of each plant name should be indicated, and whenever possible a literal translation should be provided as well (Alexiades, 1996). Furthermore, there should be a distinction between the name given to the whole plant and the name given to the plant's part, organ, or product. Moreover, vernacular plant names should always be cross-checked and voucher specimens should be collected such that the collected name can always be traced back to a herbarium specimen (Cunningham, 2001). The names listed here are not obtained out of first hand but derived from literature and no voucher specimens are attached to most of the names. In addition, some of the literature is very old and written well before thorough ethnobotanical practice was established. This means that it is very difficult to guarantee that all names have been transcribed correctly out of the different languages. Nevertheless, the list presented here, with all its shortcomings, is the most comprehensive overview so far of vernacular names in one of the largest Neotropical genera of woody trees. It is part of a so far unpublished family-wide list of vernacular names of Annonaceae species compiled by Erik Mennaga at the Nationaal Herbarium Nederland – Utrecht University branch (NHN-U). He documented these names throughout his many years of work on Taxonomic Literature (Stafleu & Mennega, 1992) and his Bibliography of the Annonaceae (Mennega, 1993) until his early death in 1994. The index published here, contains his original list and was updated for the years 1994-2006. It has to be mentioned that vernacular names from species occurring in the Guiana's are overrepresented in the indices. This is not because many more species of *Guatteria* occur there but because historically staff of the Utrecht herbarium has always been strongly involved in research in that area (for instance via the Flora of the Guiana's project or the Flora of Suriname).

From this data, four indices were compiled: (1) an index of scientific plant names in alphabetical order with all vernacular names listed together with the appropriate reference, (2) a list of alphabetized vernacular names, listed with the corresponding species name and reference, (3) a scientific species names list per geographic area, and (4) a vernacular names list per geographic area. The scientific species names lists might be most useful for the trained botanical researcher who wants to look up local names. The vernacular names lists are meant for the non-botanist who might be unfamiliar with Latin botanical names.

Vernacular names of 73 species (c. 25%) out of c. 290 *Guatteria* species are described in the indices (including vernacular names of species of the small genera *Guatteriopsis* and *Guatteriella*, that should be synonymized with *Guatteria*; this thesis, chapter 5). All scientific plant names were updated according to the Annonbase database (Maas & al., 1994; Rainer & Chatrou, 2006). Published species names that have been synonymized are listed under their currently accepted name with the species name of the original publication between brackets, e.g. *Guatteria wachenheimii* (=*G. microsperma*). The country where the name is used is always indicated and if known language (or tribe) as well. Languages were abbreviated as follows: Alu: Aluku; Ara: Arawak; Car: Carib; Cre: Creole; Mac: Macushi; Mir: Miraña; Mui: Mui; Muin: Muinane; Muio: Muio; Pal: Palikur; Por: Portugese; Sar: Saramaccan; Sra: Sranan; Sur: Surinamese Dutch; Tot: lengua totonaca, region de El Tajín; Uit: Uitoto; Wao: Waorani Indians; Way: Wayãpi; Yuc: Yucuna. In addition, the original reference of the name is mentioned. Alternate spellings of the same vernacular name are grouped together. Occasionally, names with otherwise identical spelling may be found with as well as without accent(s) but this is not indicated. Indices are formatted as follows:

1. Index of scientific plant names

Scientific name	***G. sandwithii* R.E.Fr.**
Geography	**Guyana**
vernacular name (language) [ref. number]	arara (Ara.) [9]

2. Index of vernacular plant names

vernacular name (language)	**jimokai** (Uit.)
Geography	**Colombia**
Scientific name [reference number]	*G. insculpta* R.E.Fr. [8]

3. Index of scientific names per geographic area

Geography	**Guyana**
Scientific name – vernacular name (language) [reference number]	G. *atra* Sandwith – black yarri yarri (Ara.) [9]; black kuyama [10]

4. Index of vernacular names per geographic area

Geography	**French Guiana**
vernacular name – *Scientific name* (language) [reference number]	apelemu'ï – *G. guianensis* (Aubl.) R.E.Fr. (Way.) [34]

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REFERENCES

Alexiades, M. N. 1996. Collecting ethnobotanical data: an introduction to basic concepts and techniques. Pp. 53-94 in: Alexiades, M. N. (eds.), *Selected guidelines for ethnobotanical research: a field manual*, The New York Botanical Garden, New York, U.S.A.

Cunningham, A. B. 2001. *Applied ethnobotany. People, wild plant use and conservation*. Earthscan Publications Ltd., UK and USA.

Frodin, D. G. 2004. History and concepts of big plant genera. *Taxon* 53: 753-776.

Maas, P. J. M., Mennega, E. A. & Westra, L. Y. T. 1994. Studies in Annonaceae. XXI. Index to species and infraspecific taxa of neotropical Annonaceae. *Candollea* 49: 389-481.

Mennega, E. A. 1993. *Bibliography of the Annonaceae (3rd ed.) and Iconography of the Annonaceae (1st ed.)*. Austrian Academy of Sciences, Vienna, Austria.

Morawetz, W. & Waha, M. 1985. A new pollentype, C-banded and fluorochrome counterstained chromosomes, and evolution in *Guatteria* and related genera (Annonaceae). *Pl. Syst. Evol.* 150: 119-141.

Rainer, H. & Chatrou, L. W. 2006. Annonbase: World Species List of Annonaceae - version 1.0, Published on the internet: http://www.annonaceae.org and http://www.sp2000.org/

Savolainen, V., Cuénoud, P., Spichiger, R., Martinez, M. D. P., Crèvecoeur, M. & Manen, J. F. 1995. The use of herbarium specimens in DNA phylogenetics: evaluation and improvement. *Pl. Syst. Evol.* 197: 87-98.

Stafleu, F. A. & Mennega, E. A. 1992. *Taxonomic literature. A selective guide to botanical publications and collections with dates, commentaries and types. Supplement I: A-Ba. - pp. I-VIII [= 1-8]*. Koeltz, Königstein.

Wilkie, P. & Saridan, A. 1999. The limitations of vernacular names in an inventory study, Central Kalimantan, Indonesia. *Biodiv. Cons.* 8: 1457-1467.

1. INDEX OF SCIENTIFIC PLANT NAMES

- *Guatteria*
  - **Country unknown**
    - ouregou [1]
  - **Brazil**
    - cipó-ira [1]
- cipó-uira [1]
    - embuyu branco [1]
    - envira [1]
    - envira amarela [1]
    - envira amargosa [1]
    - envira preta [1]
    - envira preta do igapó [1]
    - enviratai [1]
    - envireira [1]
    - envireira fraca [1]
    - juruá cacáuo [1]
    - laranjinha [1]
    - pindaiba [1]
  - **Colombia**
    - solera [1]
  - **Costa Rica**
    - anonillo [1]
  - **Ecuador**
    - yais [2]
  - **Guyana**
    - arara [1]
    - black kuyama [1]
    - kadaburichi [1]
    - karemero [1]
  - **Haiti**
    - bois noir [1]
  - **Mexico**
    - eklemuy [1]
    - elemuy [1]
    - elemuy box [1]
    - pusamat-kiui (Tot.) [3]
  - **Panama**
    - malagueto [1]
    - malagueto prieto [1]
  - **Peru**
    - ag-guio [1]
    - anonilla [1]
    - carahuasca [1, 4]
    - charahuaca [1]
    - envira [1]
    - espintana negra [1]
    - espintanal [1]
    - icoja, icoje [1]
    - janahuasco [1]
    - tortuga-caspi [1]
    - yana-huasca [1]
    - yuno [1]
  - **Salvador**
    - flor de Guineo [1]
  - **Venezuela**
    - yalla [1]
    - yaya [1]

- *G. aeruginosa* **Standl.**
  - **Panama**
    - malagueta [5]
    - malagueto [5]

- *G. allenii* **R.E.Fr.**
  - **Panama**
    - burillo [6]

- *G. anomala* **R.E.Fr.**
  - **Mexico**
    - corcho negro [3, 7]
    - guela-dauguixi [3]
    - ijbat, ikbat [3], ijkbat [3, 7]
    - matambilla [3]
    - palo de chombo [3, 7]
    - palo de zope [3, 7]
    - zope-zope [3]
    - zopo [7]

- *G. atabapensis* **Aristeg. ex D.M. Johnson & N.A. Murray**
  - **Colombia**
    - carguero de hoja negra [8]
    - quïbojïu dujecu (Muin.) [8]

- *G. atra* **Sandwith**
  - **Guyana**
    - arara (Ara.) [9]
    - black kuyama [10]
    - black yarri yarri [9]
    - kosopa (Mac.) [9]

- *G. australis* **A. St.-Hil.**
  - **Brazil**
    - cortiça [11]
    - embiú, embui, imbiú [12]

- *G. blainii* **(Griseb.) Urb.**
  - **Cuba**
    - comolo sielago [13]
    - purio de fangal, purio fangar [13, 14]
    - purio priuto [13]
  - **Haiti**
    - bois noir [15]
  - **Hispaniola**
    - ya ya [16]
    - ya ya prietal [16]
  - **Puerto Rico**
    - haya [5]
    - haya minga [5]
    - negra lora [5]

- *G. brachypoda* **R.E.Fr.**
  - **Guyana**
    - arara (Ara.) [9]
    - black yarri yarri [9]

- *G. cargadero* **Triana & Planch.**
  - **Colombia**
    - cargadero [17]

- *G. caribaea* **Urb.**
  - **Dominica**
    - bois violon [18]
    - maho (or mahot, mahoe, mahaut) noir [18]
  - **Guadeloupe**
    - corossol-montagne [19]
    - mahot (or mahot, mahoe, mahaut) noir [12]
    - ti cachiman-bois [19]
  - **Puerto Rico**
    - haya blanca [20]
    - ya ya [20]

- *G. chiriquiensis* **R.E.Fr.**
  - **Panama**
    - burillo [6]

- *G. chlorantha* **Diels**
  - **Peru**
    - carahuasca [21]
    - espintanal [21]
    - paschaco [21]

turtuga [21]
yana huasca, yana waska [21, 22]
yúno [22]

G. citriodora **Ducke**
Brazil
laranjinha [23]
Peru
espintana [24]

G. clavigera **R.E.Fr.**
Brazil
bananinha de macaco [25]

G. conspicua **R.E.Fr.**
Suriname
djirikawa (Ara.), kirikawa (Ara.) [26, 27]
yariyari (Sra.) [27]

G. **aff.** *decurrens* **R.E.Fr.**
Colombia
buruchicu (Mui.) [8]
carguero [8]
dujïku (Uit.) [8]
jïdïra (Uit.) [8]
ñaajeku (Mui.) [8]

G. discolor **R.E.Fr.**
Brazil
envira fofa [28]
envira preta [28]
envira rolinka [28]
French Guiana
envira fofa (Por.) [29]
envira preta (Por.) [29]
envira rolinha (Por.) [29]
matau'ï (Way.) [29]
miret (Pal.) [29]

G. dusenii **R.E.Fr.**
Brazil
cortiça [30]

G. elata **R.E.Fr.**
Peru
carahuasca [24]

G. flexilis **R.E.Fr.**
Guyana
arara (Ara.) [31]
black yariyari (Cre.) [31]

G. foliosa **Benth.**
Colombia
cïbo dujecu (Muin.) [8]
carguero negro [8]

G. galeottiana **Baill.**
Mexico
cananga [3]
ma-hum-sey [3]

G. glabrescens **R.E.Fr.** (=*G. salicifolia* R.E.Fr.)
Brazil
cortiça [11]

G. gracilipes **R.E.Fr.**
Brazil
envira preta [32]
envireira preta [32]
inajarána envira [32]

G. guianensis **(Aubl.) R.E.Fr.**
French Guiana
apelemu'ï (Way.) [33]

G. heterotricha **R.E.Fr.**
Colombia
garapatta [32]

G. hyposericea **Diels**
Peru
carahuasca [24]
chuchuhuasca-mashan [34]
yana huasca [34]

G. insculpta **R.E.Fr.**
Colombia
jakuo Muio [8]
jimokai (Uit.) [8]
palo de perfume [8]

G. inundata **Mart.**
Brazil
envira preta [32]
envireira preta do igapó, invireira preta do igapó [12], envira preta do igapó [12, 32]

G. kuhlmannii **R.E.Fr.**
Colombia
jaacu (Muin.) [8]
jimogï (Uit.) [8]

G. liesneri **D.M. Johnson & N.A. Murray**
Colombia
jïrïda (Uit.) [8]

G. lutea **A. St.-Hil.**
Brazil
imbiú [12]
imbiú amarelo [12]

G. macrocarpa **R.E.Fr.**
Colombia
buutruchicu (Mui.) [8]
puicaidoai (Uit.) [8]
Peru
hicoja negra [35]

G. macropus **Mart.**
Brazil
meiú preto [36]

G. maypurensis **Kunth** (=*G. maypurensis* Kunth var. *attenuata* R.E.Fr.)
Brazil
embiratauka [28]
enviratauka [28]

G. megalophylla **Diels**
Colombia
iyuku dujeku (Muin.) [8]
Peru
envira [32]

G. metensis **R.E.Fr.**
Venezuela
laurel majagüillo [37]

G. micans **R.E.Fr.**
Brazil
envira [32]

G. microcarpa **Ruiz & Pav.**
Peru
tortuga caspi [34]

G. modesta **Diels**
Peru
carahuasca [24]
espinal [34]
espinatana [22]

G. moralesii **(M. Gómez) Urb.**
Cuba
purio prieto [14]

G. neglecta **R.E.Fr.**
Brazil
cortiça [30]

G. nigrescens **Mart.**
Brazil
embeú preto [36]
embira preta [36]
embira vermelha [36]
embúi [36]
pindaíba preta, pindaki ba prata [12, 36]

G. odorata **R.E.Fr.**
Brazil
envira preta [32]

G. olivacea **R.E.Fr.**
Brazil
envira fofa [38]

G. oliviformis **Donn. Smith**
Costa Rica
anonillo [5]

G. ouregou **(Aubl.) Dunal**
Brazil
cananga mirim [36]
envira [12]
ouregou, ouregu [12]
Guyana
black kuyama [39]
karemero [39]

G. ovalifolia **R.E.Fr.**
Guyana
arara (Ara.) [9]
black yarri yarri [9]

G. parviflora **R.E.Fr.**
Brazil
cortiça [30]

G. parvifolia **R.E.Fr.** (=*G. flava* A. St.-Hil.)
Brazil
pindaíba preta [12]
ponte alta [40]

G. peruviana **R.E.Fr.**
Colombia
kadumïku (Muin.) [8]

G. phanerocampta **Diels**
Peru
cara huasca, charahuasca [34]

***G. pleiocarpa* Diels**
Peru
anonia [35]

***G. poeppigiana* Mart.**
Brazil
envira amarela [5]
envira amargosa [28]
envira preta [5]
invireíra [12]

***G. polyantha* R.E.Fr.**
Brazil
envira amarela [32]

***G. procera* R.E.Fr.**
Brazil
envira amarela [28]
envira preta [28]
envira surucucu [12]
Guyana
arara (Ara.) [9]
black yarri yarri [9]

***G. punctata* (Aubl.) R.A.Howard** (=*G.chrysopetala* (Steud.) Miq.)
Brazil
envira preta [28]
envira surucucu [28]
Guyana
arara (Ara.) [9]
black yarri yarri (Ara.) [9]
Suriname
baaka pau (Sar.) [van Andel, T.R., pers. comm.]
boesi-soensaka (Sur.) [41]
boszuurzak (Sur.) [27]
mamaai (Sar.) [van Andel, T.R., pers. comm.]

***G.* aff. *puncticulata* R.E.Fr.**
Colombia
faatïmïcï (Muin.) [8]

***G. rigidipes* R.E.Fr.**
Venezuela
malagueto [42]

***G. rufotomentosa* R.E.Fr.** (=*G. rufa* Triana & Planch.)
Country unknown
brown-leaved *Guatteria* [43]

***G. scandens* Ducke**
Brazil
cipó uíra, cipó-ira [12, 23]
French Guiana
cipó-ira (Por.), cipó-iuira (Por.) [29]
ndulu-ndulu (Alu.) [29]
wime etni kamwi (Pal.) [29]
Guyana
yoarno [10]
Suriname
bosolijf (Sur.) [27]
kasalerodañ (Ara.) [27]
kirikahu (Ara.) [41]
kofibali (Sur.), kufiballi (Ara.) [27, 41]
moerewa (Car). [44]
olijf (Sur.) [27, 41]
olijfrank (Sur.) [44]

***G. schlechtendaliana* Mart.**
Brazil
banana de macaco [45]

***G. schomburgkiana* Mart.**
Brazil
embira preta [46]
embira vermelha [46]
imbira [46]
maria preta [46]
Guyana
arara (Ara.) [9, 31]
black maho [31]
black yariyari (Cre.) [9, 31]
koyechi [31]
kudibutshi [39]
payuriran [31]
wayiru (Car.) [31]
yaroyaro (Car.) [31]
Suriname
arara (Ara.) [44]
araraballi (Ara.) [27]
aremenango wéwé (Car.) [27, 44]
baaha koengé (Sar.), baahaan koengé (Sar.) [44], baakakungè (Sar.) [27]
boszuurzak (Sur.), boschzuurzak (Sur.) [27, 44]
busisunsaka (Sra.) [27]
jaro jaro (Car.) [44]
koeliki kojoko karau bandihoro (Ara.), korikie kojoko kazau bandihore (Ara.) [44]
krukurutitei (Sra.) [27]
kurihi koyoko (Ara.) [27]
kurihi koyoko ferobero (Ara.) [27]
kurihi koyoko karau (Ara.) [27]
kwiengé (Sar.) [27]
maboballi wadilikoro (Ara.) [27, 44]
pajoelerian (Car.), pajoerian (Car.) [44], payuriran (Car.), payurirang (Car.) [27]
panta (Sur.) [41]
pegrekoe (Sra.), pegreku (Sra.) [27, 44]
sabana pegrekoe (Sra.), savanne pegreku (Sur.) [27, 44]
wajoeli (Car.) [44]
yaroyaro (Car., Ara.?) [27]
Venezuela
ya ya [47]

***G. schomburgkiana* Mart. var. *holosericea* R.E.Fr.**
Peru
ag-guio [34]

***G.* cf. *schunkevigoi* D.R.Simpson**
Ecuador
menedowe (Wao.) [48]

***G. slateri* Standl.**
Panama
malagueta prieto, malagueto prieto [5]

***G. spectabilis* Diels**
Peru
carawasca [22]

***G. sphaerantha* R.E.Fr.**
Colombia
carguero [8]

***G. stipitata* R.E.Fr.**
Colombia
dujeko (Yuc.) [8]
jïrïra (Uit.) [8]

***G. trichoclonia* Diels**
Colombia
jïdïra (Uit.) [8]
jïrïdaïtiyicaï (Uit.) [8]

***G. villosissima* A. St.-Hil.**
Brazil
embira branca [49]
embira de caçador [49]
pindaíba, pindakiba [36, 49]
pinxiricum [12]

***G. wachenheimii* Benoist** (=*G. microsperma* R.E.Fr.)
Suriname
panta [26]

G. sp.
Brazil
ata brava [50]
banana brava [50]
cunduru [50]
embira preta [46]
embiriba [49]
envira amarela [38]
maria preta [46]
Colombia
cargadera [51]
ñaatraje dujeku (Muin.) [8]
kïbojïu du jeko (Muin.) [8]
Guyana
arara (Ara.) [31]
black maho (Cre.) [31]
kuyama [31]
yarayara (Car.) [31]
Peru
carahuasca bajo [21]
charahusca [21]
enviha [21]
jana huasca [21]
zorro caspi [52]
Suriname
arara (Ara.) [27]
araraballi (Ara.) [27]

***Guatteriella tomentosa* R.E.Fr.**
Colombia
butruchicu (Muin.) [8]
kïyïmeko (Mir.) [8]

***Guatteriopsis blepharophylla* (Mart.) R.E. Fr.** (=*Guatteriopsis sessiliflora* Benth. R.E.Fr.)
Peru
auca hicoja [35]
carahuasca [4]

2. INDEX OF VERNACULAR PLANT NAMES

- **ag-guio**
  - **Peru**
    - *Guatteria* [1]
    - *G. schomburgkiana* Mart. var. *holosericea* R.E.Fr. [34]

- **anonia**
  - **Peru**
    - *G. pleiocarpa* Diels [35]

- **anonilla, anonillo**
  - **Costa Rica**
    - *Guatteria* [1]
    - *G. oliviformis* Donn. Smith [5]
  - **Peru**
    - *Guatteria* [1]

- **apelemu'ï** (Way.)
  - **French Guiana**
    - *G. guianensis* (Aubl.) R.E.Fr. [33]

- **arara** (Ara.)
  - **Guyana**
    - *Guatteria* [1]
    - *G. atra* Sandwith [9]
    - *G. brachypoda* R.E.Fr. [9]
    - *G. punctata* (Aubl.) R.A.Howard [9]
    - *G. flexilis* R.E.Fr. [31]
    - *G. ovalifolia* R.E.Fr. [9]
    - *G. procera* R.E.Fr. [9]
    - *G. schomburgkiana* Mart. [44]
    - *G. sp.* [31]
  - **Suriname**
    - *G. schomburgkiana* Mart. [9, 31]
    - *G. sp.* [27]

- **araraballi** (Ara.)
  - **Suriname**
    - *G. schomburgkiana* Mart. [27]
    - *G. sp.* [27]

- **aremenango wéwé** (Car.)
  - **Suriname**
    - *G. schomburgkiana Mart.* [27, 44]

- **ata brava**
  - **Brazil**
    - *G. sp.* [50]

- **auca hicoja**
  - **Peru**
    - *Guatteriopsis blepharophylla* (Mart.) R.E. Fr. (=*Guatteriopsis sessiliflora* Benth. R.E.Fr.) [35]

- **baaha koengé** (Sar.)**, baahaan koengé** (Sar.), **baakakungè** (Sar.)
  - **Suriname**
    - *G. schomburgkiana* Mart. [27, 44]

- **baaka pau** (Sar.)
  - **Suriname**
    - *G. punctata* (Aubl.) R.A.Howard [van Andel, T.R., pers. comm.]

- **banana de macaco, bananinha de macaco**
  - **Brazil**
    - *G. clavigera* R.E.Fr. [25]
    - *G. schlechtendaliana* Mart. [45]

- **banana brava**
  - **Brazil**
    - *G. sp.* [50]

- **black kuyama**
  - **Guyana**
    - *Guatteria* [1]
    - *G. atra* Sandwith [10]
    - *G. ouregou* (Aubl.) Dunal [39]

- **black maho**
  - **Guyana**
    - *G. schomburgkiana* Mart. [31]
    - *G. sp.* (Cre.) [31]

- **black yariyari** (Cre.)**, black yarri yarri** (Ara.)
  - **Guyana**
    - *G. atra* Sandwith [9]
    - *G. brachypoda* R.E.Fr. [9]
    - *G. flexilis* R.E.Fr. [31]
    - *G. punctata* (Aubl.) R.A.Howard [9]
    - *G. ovalifolia* R.E.Fr. [9]
    - *G. procera* R.E.Fr. [9]
    - *G. schomburgkiana* Mart. [9, 31]

- **boesi-soensaka** (Sur.)
  - **Suriname**
    - *G. punctata* (Aubl.) R.A.Howard (=*G.chrysopetala* (Steud.) Miq.) [41]

- **bois noir**
  - **Haiti**
    - *Guatteria* [1]
    - *G. blainii* (Griseb.) Urb. [15]

- **bois violon**
  - **Dominica**
    - *G. caribaea* Urb. [18]

- **boszuurzak** (Sur.), **boschzuurzak** (Sur.)
  - **Suriname**
    - *G. schomburgkiana* Mart. [27, 44]
    - *G. punctata* (Aubl.) R.A.Howard [27]

- **bosolijf** (Sur.)
  - **Suriname**
    - *G. scandens* Ducke [27]

- **brown-leaved *Guatteria***
    - *G. rufotomentosa* R.E.Fr. (=*G. rufa* Triana & Planch.) [43]

- **burillo**
  - **Panama**
    - *G. allenii R.E.Fr.* [6]
    - *G. chiriquiensis* R.E.Fr. [6]

- **buruchicu** (Mui.), **butruchicu** (Mui.), **buutruchicu** (Mui.)
  - **Colombia**
    - *G.* aff. *decurrens* R.E.Fr. [8]
    - *G. macrocarpa* R.E.Fr. [8]
    - *Guatteriella tomentosa* R.E.Fr. [8]

- **busisunsaka** (Sra.)
  - **Suriname**
    - *G. schomburgkiana* Mart.[27]

- **cïbo dujecu** (Mui.)
  - **Colombia**
    - *G. foliosa* Benth. [8]

- **cananga**
  - **Mexico**
    - *G. galeottiana* Baill. [3]

- **cananga mirim**
  - **Brazil**
    - *G. ouregou* (Aubl.) Dunal [36]

- **carahuasca, cara huasca, carawasca**
  - **Peru**
    - *Guatteria* [1, 4]
    - *G. chlorantha* Diels (**Peru**) [21]
    - *G. elata* R.E.Fr. [24]
    - *G. hyposericea* Diels [24]
    - *G. modesta* Diels [24]
    - *G. phanerocampta* Diels [34]
    - *G. spectabilis Diels* [22]
    - *Guatteriopsis blepharophylla* (Mart.) R.E. Fr. (=*Guatteriopsis sessiliflora* Benth. R.E.Fr.) [4]

- **carahuasca bajo**
  - **Peru**
    - *G. sp.* [21]

- **cargadera, cargadero**
  - **Colombia**
    - *G. cargadero* Triana & Planch. [17]
    - *G. sp.* [51]

- **carguero**
  - **Colombia**
    - *G.* aff. *decurrens* R.E.Fr. [8]
    - *G. sphaerantha R.E.Fr.* [8]

- **carguero de hoja negra**
  - **Colombia**
    - *G. atabapensis* Aristeg. ex D.M. Johnson & N.A. Murray [8]

- **carguero negro**
  - **Colombia**
    - *G. foliosa* Benth. [8]

charahuaca, charahuasca, charahusca
Peru
Guatteria [1]
G. phanerocampta Diels [34]
G. sp. [21]

chuchuhuasca-mashan
Peru
G. hyposericea Diels [34]

Brazil
G. scandens Ducke [12]

cipó uíra, cipó-ira, cipó-iuira (Por.), **cipó-uira**
Brazil
Guatteria [1]
French Guiana
G. scandens Ducke (Por.) [23, 29]

comolo sielago
Cuba
G. blainii (Griseb.) Urb. [13]

corcho negro
Mexico
G. anomala R.E.Fr. [3, 7]

corossol-montagne
Guadeloupe
G. caribaea Urb. [19]

cortiça
Brazil
G. australis A. St.-Hil. [11]
G. dusenii R.E.Fr. [30]
G. neglecta R.E.Fr. [30]
G. parviflora R.E.Fr. [30]
G. glabrescens R.E.Fr. (=*G. salicifolia* R.E.Fr.) [11]

cunduru
Brazil
G. sp. [50]

djirikawa (Ara.)
Suriname
G. conspicua R.E.Fr. [26]

dujeko (Yuc.), **dujïku** (Uit.)
Colombia
G. aff. *decurrens* R.E.Fr. [8]
G. stipitata R.E.Fr. [8]

eklemuy, elemuy
Mexico
Guatteria [1, 13]

elemuy box
Mexico
Guatteria [1]

embeú preto
Brazi
G. nigrescens Mart. [36]

embira branca
Brazil
G. villosissima A. St.-Hil. [49]

embira de caçador
Brazil
G. villosissima A. St.-Hil. [49]

embira preta, envira preta
Brazil
Guatteria [1]
G. discolor R.E.Fr. [28, 29]
G. gracilipes R.E.Fr. [32]
G. inundata Mart. [32]
G. nigrescens Mart. [36]
G. odorata R.E.Fr. [32]
G. poeppigiana Mart. [5]
G. punctata (Aubl.) R.A.Howard [28]
G. procera R.E.Fr. [28]
G. schomburgkiana Mart.[46]
G. sp. [46]

embira vermelha
Brazil
G. nigrescens Mart. [36]
G. schomburgkiana Mart.[46]

embiratauka
Brazil
G. maypurensis Kunth (=*G. maypurensis* Kunth var. *attenuata* R.E.Fr.) [28]

embiriba
Brazil
G. sp. [49]

embiú, embui, embúi
Brazil
G. australis A. St.-Hil. [12]
G. nigrescens Mart. [36]

embuyu branco
Brazil
Guatteria [1]

envira, enviha

Brazil
Guatteria [1]
G. micans R.E.Fr. [32]
G. ouregou (Aubl.) Dunal [12]
Peru
Guatteria [1]
G. megalophylla Diels [32]
G. sp. [21]

envira amarela
Brazil
Guatteria [1]
G. poeppigiana Mart. [5]
G. polyantha R.E.Fr. [32]
G. procera R.E.Fr. [28]
G. sp. [38]

envira amargosa
Brazil
Guatteria [1]
G. poeppigiana Mart. [28]

envira fofa
Brazil
G. discolor R.E.Fr. [28, 29]
G. olivacea R.E.Fr. [38]

envira preta do igapó
Brazil
Guatteria [1]
G. inundata Mart. [12, 32]

envira rolinka, envira rolinha (Por.)
Brazil
G. discolor R.E.Fr. [28]
French Guiana
G. discolor R.E.Fr. [29]

envira surucucu
Brazil
G. punctata (Aubl.) R.A.Howard [28]
G. procera R.E.Fr. [12]

enviratai
Brazil
Guatteria [1]

envirataukа
Brazil
G. maypurensis Kunth (=*G. maypurensis* Kunth var. *attenuata* R.E.Fr.) [28]

envireira
Brazil
Guatteria [1]

envireira fraca
Brazil
Guatteria [1]

envireira preta
Brazil
G. gracilipes R.E.Fr. [32]

envireira preta do igapó
Brazil
G. inundata Mart. [12]

espinal
Peru
G. modesta Diels [34]

espintana, espinatana
Peru
G. citriodora Ducke [24]
G. modesta Diels [22]

espintana negra
Peru
Guatteria [1]

espintanal
Peru
Guatteria [1]
G. chlorantha Diels [21]

faatïmïcï (Mui.)
Colombia
G. aff. *puncticulata* R.E.Fr. [8]

flor de Guineo
Salvador
Guatteria [1]

garapatta
Colombia
G. heterotricha R.E.Fr. [32]

guela-dauguixi
Mexico
G. anomala R.E.Fr. [3]

haya
Puerto Rico
G. blainii (Griseb.) Urb. [5]

haya blanca
Puerto Rico
G. caribaea Urb. [20]

haya minga
Puerto Rico
G. blainii (Griseb.) Urb. [5]

hicoja negra
Peru
G. macrocarpa R.E.Fr. [35]

icoja, icoje
Peru
Guatteria [1]

ijbat, ijkbat, ikbat
Mexico
G. anomala R.E.Fr. [3, 7]

imbira
Brazill
G. schomburkiana Mart. [46]

imbiú
Brazil
G. australis A. St.-Hil. [12]
G. lutea A. St.-Hil. [12]

imbiú amarelo
Brazil
G. lutea A. St.-Hil. [12]

inajarána envira
Brazil
G. gracilipes R.E.Fr. [32]

invireíra
Brazil
G. poeppigiana Mart. [12]

invireira preta do igapó
Brazil
G. inundata Mart. [12]

iyuku dujeku (Mui.)
Colombia
G. megalophylla Diels [8]

jïdïra (Uit.)
Colombia
G. aff. *decurrens* R.E.Fr. [8]
G. trichoclonia Diels [8]

jïrïda (Uit.)
Colombia
G. liesneri D.M. Johnson & [8]

jïrïdaïtiyicaï (Uit.)
Colombia
G. trichoclonia Diels [8]

jïrïra (Uit.)
Colombia
G. stipitata R.E.Fr. [8]

jaacu (Mui.)
Colombia
G. kuhlmannii R.E.Fr. [8]

jakuo (Mui.)
Colombia
G. insculpta R.E.Fr. [8]

jana huasca, janahuasco
Peru
Guatteria [1]
G. sp. [21]

jaro jaro (Car.)
Suriname
G. schomburgkiana Mart. [44]

jimogï (Uit.)
Colombia
G. kuhlmannii R.E.Fr. [8]

jimokai (Uit.
Colombia
G. insculpta R.E.Fr. [8]

juruá cacáuo
Brazil
Guatteria [1]

kïbojïu du jeko (Mui.)
Colombia
G. sp. [8]

kïyïmeko (Mir.)
Colombia
Guatteriella tomentosa R.E.Fr. [8]

kadaburichi
Guyana
Guatteria [1]

kadumïku (Mui.)
Colombia
G. peruviana R.E.Fr. [8]

karemero
Guyana
Guatteria [1]
G. ouregou (Aubl.) Dunal [39]

kasalerodañ (Ara.)
Suriname
G. scandens Ducke [27]

kirikahu (Ara.)
Suriname
G. scandens Ducke [41]

kirikawa
Suriname
G. conspicua R.E.Fr. (Ara.) [27]
G. scandens Ducke (Sra.) [27]

koeliki kojoko karau bandihoro (Ara.), **korikie kojoko kazau bandihore** (Ara.), **kurihi koyoko karau bandikoro** (Ara.)
Suriname
G. schomburgkiana Mart. [27, 44]

kofibali (Sur.), **kufiballi** (Ara.)
Suriname
G. scandens Ducke [27, 41]

kosopa (Mac.)
Guyana
G. atra Sandwith [9]

koyechi
Guyana
G. schomburgkiana Mart. [31]

krukurutitei (Sra.)
Suriname
G. schomburgkiana Mart. [27]

kudibutshi
Guyana
G. schomburgkiana Mart. [39]

kurihi koyoko (Ara.)
Suriname
G. schomburgkiana Mart. [27]

kurihi koyoko ferobero (Ara.)
Suriname
G. schomburgkiana Mart. [27]

kuyama
Guyana
G. sp. [31]

kwiengé (Sar.)
Suriname
G. schomburgkiana Mart. [27]

laranjinha
Brazil
Guatteria [1]
G. citriodora Ducke [23]

laurel majagüillo
Venezuela
G. metensis R.E.Fr. [37]

maboballi wadilikoro (Ara.)
Suriname
G. schomburgkiana Mart. [27, 44]

maho (or mahot, mahoe, mahaut) noir
Dominica
G. caribaea Urb. [18]
Guadeloupe
G. caribaea Urb. [12]

ma-hum-sey
Mexico
G. galeottiana Baill. [3]

malagueta, malagueto
- **Panama**
  - *Guatteria* [1]
  - *G. aeruginosa* Standl. [5]
- **Venezuela**
  - *G. rigidipes* R.E.Fr. [42]

malagueta prieto, malagueto prieto
- **Panama**
  - *Guatteria* [1]
  - *G. slateri* Standl. [5]

mamaai (Sar.)
- **Suriname**
  - *G. punctata* (Aubl.) R.A.Howard [van Andel, T.R., pers. comm.]

maria preta
- **Brazil**
  - *G. schomburgkiana* Mart. [46]
  - *G. sp.* [46]

matambilla
- **Mexico**
  - *G. anomala* R.E.Fr. [3]

matau'ï (Way.)
- **French Guiana**
  - *G. discolor* R.E.Fr. [29]

meiú preto
- **Brazil**
  - *G. macropus* Mart. [36]

menedowe (Wao.)
- **Ecuador**
  - *G.* cf. *schunkevigoi* D.R.Simpson [48]

miret (Pal.)
- **French Guiana**
  - *G. discolor* R.E.Fr. [29]

moerewa
- **Suriname** (Car.)
  - *G. scandens* Ducke [44]

ñaajeku (Mui.)
- **Colombia**
  - *G.* aff. *decurrens* R.E.Fr. [8]

ñaatraje dujeku (Mui.)
- **Colombia**
  - *G. sp.* [8]

ndulu-ndulu (Alu.)
- **French Guiana**
  - *G. scandens* Ducke [29]

negra lora
- **Puerto Rico**
  - *G. blainii* (Griseb.) Urb. [5]

olijf (Sur.)
- **Suriname**
  - *G. scandens* Ducke [27, 41]

olijfrank (Sur.)
- **Suriname**
  - *G. scandens* Ducke [44]

ouregou, ouregu
- **Country unknown**
  - *Guatteria* [1]
- **Brazil**
  - *G. ouregou* (Aubl.) Dunal [12]

pajoelerian (Car.)**, pajoerian** (Car.), **payuriran, payuri-rang** (Car.)
- **Guyana**
  - *G. schomburgkiana* Mart. [31]
- **Suriname**
  - *G. schomburgkiana* Mart. [27, 44]

palo de chombo
- **Mexico**
  - *G. anomala* R.E.Fr. [3, 7]

palo de perfume
- **Colombia**
  - *G. insculpta* R.E.Fr. [8]

palo de zope, palo de zopo
- **Mexico**
  - *G. anomala* R.E.Fr. [3, 7]

panta
- **Suriname**
  - *G. schomburgkiana* Mart. (Sur.) [41]
  - *G. wachenheimii* Benoist (=*G. microsperma* R.E.Fr.) [26]

paschaco
- **Peru**
  - *G. chlorantha* Diels [21]

pegrekoe (Sra.), **pegreku** (Sra.)
- **Suriname**
  - *G. schomburgkiana* Mart. [27, 44]

pindaiba, pindaíba
- **Brazil**
  - *Guatteria* [1]
  - *G. villosissima* A. St.-Hil. [49]

pindaíba preta
- **Brazil**
  - *G. parvifolia* R.E.Fr. (=*G. flava* A. St.-Hil.) [12]
  - *G. nigrescens* Mart. [12]

pindaki ba prata
- **Brazil**
  - *G. nigrescens* Mart. [36]

pindakiba
- **Brazil**
  - *G. villosissima* A. St.-Hil. [36]

pinxiricum
- **Brazil**
  - *G. villosissima* A. St.-Hil. [12]

ponte alta
- **Brazil**
  - *G. parvifolia* R.E.Fr. [40]

puicaidoai (Uit.)
- **Colombia**
  - *G. macrocarpa* R.E.Fr. [8]

purio de fangal
- **Cuba**
  - *G. blainii* (Griseb.) Urb. [13]

purio fangar
- **Cuba**
  - *G. blainii* (Griseb.) Urb. [14]

purio prieto, purio priuto
- **Cuba**
  - *G. blainii* (Griseb.) Urb. [13]
  - *G. moralesii* (M. Gómez) Urb. [14]

pusamat-kiui (Tot.)
- **Mexico**
  - *Guatteria* [3]

quïbojïu dujecu (Mui.)
- **Colombia**
  - *G. atabapensis* Aristeg. ex D.M. Johnson & N.A. Murray [8]

sabana pegrekoe (Sra.), **savanne pegreku** (Sur.)
- **Suriname**
  - *G. schomburgkiana Mart.* [27, 44]

solera
- **Colombia**
  - *Guatteria* [1]

ti cachiman-bois
- **Guadeloupe**
  - *G. caribaea* Urb. [19]

tortuga caspi
- **Peru**
  - *Guatteria* [1]
  - *G. microcarpa* Ruiz & Pav. [34]

turtuga
- **Peru**
  - *G. chlorantha* Diels [21]

wajoeli (Car.)
- **Suriname**
  - *G. schomburgkiana* Mart. [44]

wayiru (Car.)
- **Guyana**
  - *G. schomburgkiana* Mart. [31]

wime etni kamwi (Pal.)
- **French Guiana**
  - *G. scandens* Ducke [29]

ya ya
- **Hispaniola**
  - *G. blainii* (Griseb.) Urb. [16]
  - *G. caribaea* Urb. [20]
- **Puerto Rico**
  - *Guatteria* [1]
- **Venezuela**
  - *G. schomburgkiana* Mart.

[47]

ya ya prietal
Hispaniola
G. blainii (Griseb.) Urb. [16]

yais
Ecuador
Guatteria [2]

yalla
Venezuela
Guatteria [1]

yana huasca, yana waska
Peru
Guatteria [1]
G. chlorantha Diels [21, 22]
G. hyposericea Diels [34]

yarayara (Car.)
Guyana
G. sp. [31]

yariyari (Sra.)
Suriname
G. conspicua R.E.Fr. [27]

yaroyaro (Car., Ara.?)
Guyana
G. schomburgkiana Mart. [31]
Suriname
G. schomburgkiana Mart. [27]

yoarno
Guyana
G. scandens Ducke [10]

yuno, yúno
Peru
Guatteria [1]
G. chlorantha Diels [22]

zope-zope
Mexico
G. anomala R.E.Fr. [3]

zopo
Mexico
G. anomala R.E.Fr. [7]

zorro caspi
Peru
G. sp. [52]

3. INDEX OF SCIENTIFIC NAMES PER GEOGRAPHIC AREA

Country unknown
Guatteria – ouregou [1]
G. rufotomentosa R.E.Fr. (=*G. rufa* Triana & Planch.) – brown-leaved *G.* [43]
G. scandens Ducke – kirikahu (Ara.) [41]

Brazil
Guatteria – juruá cacáuo, cipó-uira, embuyu branco, envira amarela, envira preta, envira preta do igapó, enviratai, envireira fraca, envira, laranjinha, pindaiba, cipó-ira, envireira, envira amargosa [1]
G. australis A. St.-Hil. – cortiça [11]; embui, embiú, imbiú [12]
G. citriodora Ducke – laranjinha [23]
G. clavigera R.E.Fr. – bananinha de macaco [25]
G. discolor R.E.Fr. – envira rolinka, envira preta, envira fofa [28]
G. dusenii R.E.Fr. – cortiça [30]
G. glabrescens R.E.Fr. (=*G. salicifolia* R.E.Fr.) – cortiça [11]
G. gracilipes R.E.Fr. – envireira preta, inajarána envira, envira preta [32]
G. inundata Mart. – envira preta [32]; envira preta do igapó [12, 32], envireira preta do igapó, invireira preta do igapó [12]
G. lutea A. St.-Hil. – imbiú, imbiú amarelo [12]
G. macropus Mart. – meiú preto [36]
G. maypurensis Kunth (=*G. maypurensis* Kunth var. *attenuata* R.E.Fr.) – embiratauka, enviratauka [28]
G. micans R.E.Fr. – envira [32]
G. neglecta R.E.Fr. – cortiça [30]
G. nigrescens Mart. – pindaki ba prata, embira preta, embira vermelha, embúi, embeú preto [36]; pindaíba preta [12]
G. odorata R.E.Fr. – envira preta [32]
G. olivacea R.E.Fr. – envira fofa [38]
G. ouregou (Aubl.) Dunal ouregu, ouregou, envira [12]; cananga mirim [36]
G. parviflora R.E.Fr. – cortiça [30]
G. parvifolia R.E.Fr. (=*G. flava* A. St.-Hil.) – pindaíba preta [12]; ponte alta [40]
G. poeppigiana Mart. – invireíra, [12]; envira preta, envira amarela [5]; envira amargosa [28]
G. polyantha R.E.Fr. – envira amarela [32]
G. procera R.E.Fr. – envira surucucu [12]; envira amarela, envira preta [28]
G. punctata (Aubl.) R.A.Howard – envira preta, envira surucucu [28]
G. scandens Ducke – cipó-ira [23]; cipó uíra [12]
G. schlechtendaliana Mart. – banana de macaco [45]
G. schomburgkiana Mart. – embira preta, embira vermelha, imbira, maria preta [46]
G. sp. – ata brava, banana brava, cunduru [50]; embiriba [49]; embira preta, maria preta [46]; envira amarela [38]
G. villosissima A. St.-Hil. – embira branca, embira de caçador, pindaíba [49]; pinxiricum [12]; pindakiba [36]

Guyana
Guatteria – arara, black kuyama, kadaburichi, karemero [1]
G. atra Sandwith – arara (Ara.), black yarri yarri, kosopa (Mac.) [9]; black kuyama [10]
G. brachypoda R.E.Fr. – arara (Ara.), black yarri yarri [9]
G. ouregou (Aubl.) Dunal – black kuyama, karemero [39]
G. ovalifolia R.E.Fr. – arara (Ara.), black yarri yarri [9]
G. procera R.E.Fr. – arara (Ara.), black yarri yarri [9]
G. punctata (Aubl.) R.A.Howard – arara (Ara.), black yarri yarri (Ara.) [9]
G. scandens Ducke – yoarno [10]
G. schomburgkiana Mart. – arara (Ara.), black yarri yarri [9]; kudibutshi [39]

Colombia
Guatteria – solera [1]
G. atabapensis Aristeguieta ex D.M. Johnson & N.A. Murray – carguero de hoja negra, quïbojïu dujecu (Mui.) [8]
G. cargadero Triana & Planch. – cargadero [17]
G. aff. *decurrens* R.E.Fr. – buruchicu (Mui.), carguero, dujïku (Uit.), jïdïra (Uit.), ñaajeku (Mui.) [8]
G. foliosa Benth. – carguero negro, cïbo dujecu (Mui.) [8]
G. heterotricha R.E.Fr. – garapatta [32]
G. insculpta R.E.Fr. – jakuo (Mui.), jimokai (Uit.), palo de perfume [8]
G. kuhlmannii R.E.Fr. – jaacu (Mui.), jimogï (Uit.) [8]
G. liesneri D.M. Johnson & N.A. Murray – jïrïda (Uit.) [8]
G. macrocarpa R.E.Fr. – buutruchicu (Mui.), puicaidoai (Uit.)[8]
G. megalophylla Diels – iyuku dujeku (Mui.) [8]
G. peruviana R.E.Fr. – kadumïku (Mui.) [8]
G. aff. *puncticulata* R.E.Fr. – faatïmïcï (Mui.) [8]
G. sphaerantha R.E.Fr. – carguero [8]
G. stipitata R.E.Fr. – dujeko (Yuc.), jïrïra (Uit.) [8]
G. trichoclonia Diels – jïrïdaïtiyicaï (Uit.); jïdïra (Uit.) [8]
G. sp. – cargadera [51]; kïbojïu du jeko (Mui.), ñaatraje dujeku (Mui.) [8]
Guatteriella tomentosa R.E.Fr. – butruchicu (Mui.); kïyïmeko (Mir.) [8]

Costa Rica
Guatteria – anonillo [1]
G. oliviformis Donn. Smith – anonillo [5]

Cuba
G. blainii (Griseb.) Urb. – comolo

sielago, purio de fangal, purio priuto [13]; purio fangar [14]
G. moralesii (M. – Gómez) Urb. – purio prieto [14]

Dominica
G. caribaea Urb. – bois violon, maho (or mahot, mahoe, mahaut) noir [18]

Ecuador
Guatteria – yais [2]
G. cf. *schunkevigoi* D.R.Simpson – menedowe (Wao.) [48]

French Guiana
G. discolor R.E.Fr. – envira fofa (Por.), envira preta (Por.), envira rolinha (Por.), matau’ï (Way.), miret (Pal.) [29]; matau’ï (Way.), miret (Pal.) [33]
G. guianensis (Aubl.) R.E.Fr. – apelemu’ï (Way.) [33]
G. scandens Ducke – cipó-ira (Por.), cipó-iuira (Por.), ndulu-ndulu (Alu.) [29]; wime etni kamwi (Pal.) [29, 33]

Guadeloupe
G. caribaea Urb. – corossol-montagne, ti cachiman-bois [19]

Guyana
G. flexilis R.E.Fr. – arara (Ara.), black yariyari (Cre.) [31]
G. schomburgkiana Mart. – arara (Ara.), black maho, black yariyari (Cre.), koyechi, payuriran, wayiru (Car.), yaroyaro (Car.) [31]
G. sp. – arara (Ara.), black maho (Cre.), kuyama, yarayara (Car.) [31]

Haiti
Guatteria – bois noir [1]
G. blainii (Griseb.) Urb. – bois noir [15]

Hispaniola
G. blainii (Griseb.) Urb. – ya ya, ya prietal [16]

Mexico
Guatteria – eklemuy, elemuy, elemuy box [1]; pusamat-kiui (Tot.) [3]
G. anomala R.E.Fr. – ijbat, ikbat, matambilla, palo de chombo [3], zope-zope [3]; palo de zopo, zopo [7]; corcho negro, ijkbat, palo de zope [3, 7]; guela-dauguixi [3]
G. galeottiana Baill. – cananga, mahum-sey [3]

Panama
Guatteria – malagueto, malagueto prieto [1]
G. aeruginosa Standl. – malagueta, malagueto [5]
G. allenii R.E.Fr. – burillo [6]
G. chiriquiensis R.E.Fr. – burillo [6]
G. slateri Standl. – malagueta prieto, malagueto prieto [5]

Peru
Guatteria – ag-guio, anonilla, charahuaca, carahuasca, envira, espintanal, espintana negra, icoja, icoje, janahuasco, tortuga-caspi, yana-huasca, yuno [1]; carahuasca [4]
G. chlorantha Diels – carahuasca, espintanal, paschaco, turtuga, yana huasca [21]; yana waska [22], yúno [22]
G. citriodora Ducke – espintana [24]
G. elata R.E.Fr. – carahuasca [24]
G. hyposericea Diels – carahuasca [24]; chuchuhuasca-mashan, yana huasca [34]
G. macrocarpa R.E.Fr. – hicoja negra [35]
G. megalophylla Diels – envira [32]
G. microcarpa Ruiz & Pav. – tortuga caspi [34]
G. modesta Diels – carahuasca [24]; espinal [34]; espinatana [22]
G. phanerocampta Diels – cara huasca, charahuasca [34]
G. pleiocarpa Diels – anonia [35]
G. schomburgkiana Mart. var. *holosericea* R.E.Fr. – ag-guio [34]
G. spectabilis Diels – carawasca [22]
G. sp. – carahuasca bajo, charahusca, enviha, jana huasca [21]; zorro caspi [52]
Guatteriopsis blepharophylla (Mart.) R.E. Fr. (=*Guatteriopsis sessiliflora* Benth. R.E.Fr.) – carahuasca [4]
Guatteriopsis blepharophylla (Mart.) R.E. Fr. (=*Guatteriopsis sessiliflora* Benth. R.E.Fr.) – auca hicoja [35]

Puerto Rico
G. blainii (Griseb.) Urb. – haya, negra lora, haya minga [5]
G. caribaea Urb. – haya blanca, ya ya [20]

Salvador
Guatteria – flor de Guineo [1]

Suriname
G. conspicua R.E.Fr. – djirikawa (Ara.) [26]; kirikawa (Ara.), yariyari (Sra.) [27]
G. punctata (Aubl.) R.A.Howard (=*G.chrysopetala* (Steud.) Miq.) – baaka pau (Sar.), mamaai (Sar.) [van Andel, T.R., pers. – comm.]; boesi-soensaka (Sur.) [41]; boszuurzak (Sur.) [27]
G. scandens Ducke – kofibali (Sur.) [41]; olijf (Sur.) [27, 41]; bosolijf (Sur.), kasalerodañ (Ara.), kirikawa (Sra.), kufiballi (Ara.) [27]; moerewa (Car.) [44]; olyfrank (Sur.) [44]
G. schomburgkiana Mart. – panta (Sur.) [41]; araraballi (Ara.), aremenango wewe (Car.), aremenango wéwé (Car.), baakakungè (Sar.), boszuurzak (Sur.), busisunsaka (Sra.), krukurutitei (Sra.), kurihi koyoko (Ara.), kurihi koyoko ferobero (Ara.), kurihi koyoko karau bandikoro (Ara.), kwiengé (Sar.), maboballi wadilikoro (Ara.), payuriran (Car.), payuri-rang (Car.), pegreku (Sra.), savanne pegreku (Sur.), wajoeli (Car.), yaroyaro (Car., Ara.?) [27]; arara (Ara.), aremenango wéwé (Car.), baaha koengé (Sar.), baahaan koengé (Sar.), boschzuurzak (Sur.), jaro jaro (Car.), koeliki kojoko karau bandihoro (Ara.), korikie kojoko kazau bandihore (Ara.), maboballi wadilikoro (Ara.), pajoelerian (Car.), pajoerian (Car.), pegrekoe (Sra.), sabana pegrekoe (Sra.) [44]
G. wachenheimii Benoist (=*G. microsperma* R.E.Fr.) – panta [26]
G. sp. – arara (Ara.), araraballi (Ara.) [27]

Venezuela
Guatteria – yalla, yaya [1]
G. metensis R.E.Fr. – laurel majagüillo [37]
G. rigidipes R.E.Fr. – malagueto [42]
G. schomburgkiana Mart. – ya ya [47]

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Brazil
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maria preta – *Guatteria schomburgkiana* Mart. [46]; *Guatteria sp.* [46]
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Guyana
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black kuyama – *G. ouregou* (Aubl.) Dunal [39]
black yarri yarri – *G. atra* Sandwith [9]
kadaburichi – *Guatteria* [1]
karemero – *G. ouregou* (Aubl.) Dunal [39]
kosopa – *G. atra* Sandwith [9]
kudibutshi – *G. schomburgkiana* Mart. [39]
yoarno – *G. scandens* Ducke [10]

Colombia
buruchicu, butruchicu, buutruchicu – *G.* aff. *decurrens* R.E.Fr. (Mui.), *G. macrocarpa* R.E.Fr. (Mui.),*Guatteriella tomentosa* R.E.Fr. (Mui.) [8]
cïbo dujecu – *G. foliosa* Benth. (Mui.) [8]
cargadera, cargadero –*G. cargadero* Triana & [17]; *G. sp.* [51]
carguero – *G. sphaerantha* R.E.Fr. [8]
carguero de hoja negra – *G. atabapensis* Aristeg. ex D.M. Johnson & N.A. Murray [8]
carguero negro – *G. foliosa* Benth. [8]
dujeko, dujïku – *G.* aff. *decurrens* R.E.Fr. (Uit.), *G. stipitata* R.E.Fr. (Yuc.) [8]
faatïmïcï – *G.* aff. *puncticulata* R.E.Fr. (Mui.) [8]
garapatta – *G. heterotricha* R.E.Fr. [32]
iyuku dujeku – *G. megalophylla* Diels (Mui.) [8]
jïdïra – *G. trichoclonia* Diels (Uit.), *G.* aff. *decurrens* R.E.Fr. (Uit.) [8]
jïrïda – *G. liesneri* D.M. Johnson & (Uit.) [8]
jïrïdaïtiyicaï – *G. trichoclonia* Diels (Uit.) [8]
jïrïra – *G. stipitata* R.E.Fr. (Uit.) [8]
jaacu – *G. liesneri* R.E.Fr. (Mui.) [8]
jakuo – *G. insculpta* R.E.Fr. (Mui.) [8]
jimogï – *G. liesneri* R.E.Fr. (Uit.) [8]
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kïbojïu du jeko – *G. sp.* (Mui.) [8]
kïyïmeko – *Guatteriella tomentosa* R.E.Fr. (Mir.) [8]
kadumïku – *G. peruviana* R.E.Fr. (Mui.) [8]
ñaajeku – *G. sp.*B (aff. G. (Mui.) [8]
ñaatraje dujeku – *G. sp.* (Mui.) [8]
palo de perfume – *G. insculpta* R.E.Fr. [8]
puicaidoai – *G. macrocarpa* R.E.Fr. (Uit.) [8]
quïbojïu dujecu – *G. atabapensis* Aristeg. ex D.M. Johnson & N.A. Murray (Mui.) [8]
solera – *Guatteria* [1]

Costa Rica
anonillo – *G. oliviformis* Donn. [5]

Cuba
comolo sielago – *G. blainii* (Griseb.) Urb. [13]
purio de fangal – *G. blainii* (Griseb.) Urb. [13]
purio fangar – *G. blainii* (Griseb.) Urb. [14]
purio prieto, purio priuto – *G. blainii* (Griseb.) Urb. [13]; *G. moralesii* (M. Gómez) Urb. [14]

Dominica
bois violon – *G. caribaea* Urb. [18]
maho (or mahot, mahoe, mahaut) noir – *G. caribaea* Urb. [18]

Ecuador
yais – *Guatteria* [2]
menedowe – *G.* cf. *schunkevigoi* D.R.Simpson (Wao.) [48]

French Guiana
apelemu’ï – *G. guianensis* (Aubl.) (Way.) [33]
cipó-ira, cipó-iuira – *G. scandens* Ducke (Por.) [29]
envira fofa – *G. discolor* R.E.Fr. (Por.) [29]
envira preta – *G. discolor* R.E.Fr. (Por.) [29]
envira rolinha – *G. discolor* R.E.Fr. (Por.) [29]
matau’ï – *G. discolor* R.E.Fr. (Way.) [33]
miret – *G. discolor* R.E.Fr. (Pal.) [33]
ndulu-ndulu – *G. scandens* Ducke (Alu.) [29]
wime etni kamwi – *G. scandens* Ducke (Pal.) [33]

Guadeloupe
corossol-montagne – *G. caribaea* Urb. [19]
ti cachiman-bois – *G. caribaea* Urb. [19]

Guyana
arara – *G. schomburgkiana* Mart. (Ara.) [31]
black maho – *G. schomburgkiana*

Mart. [31]
black yariyari – *G. schomburgkiana* Mart. (Cre.) [31]
koyechi – *G. schomburgkiana* Mart. [31]
kuyama – *G. sp.* [31]
payuriran – *G. schomburgkiana* Mart. [31]
wayiru – *G. schomburgkiana* Mart. (Car.) [31]
yarayara – *G. sp.* (Car.) [31]
yaroyaro – *G. schomburgkiana* Mart. (Car.) [31]

Haiti
bois noir – *G. blainii* (Griseb.) Urb. [15]

Hispaniola
ya ya – *G. blainii* (Griseb.) Urb. [16]
ya ya prietal – *G. blainii* (Griseb.) Urb. [16]

Mexico
cananga – *G. galeottiana* Baill. [3]
corcho negro – *G. anomala* R.E.Fr. [3, 7]
guela-dauguixi – *G. anomala* R.E.Fr. [3]
eklemuy, elemuy – *Guatteria* [1]
elemuy box – *Guatteria* [1]
ijbat, ijkbat, ikbat – *G. anomala* R.E.Fr. [3, 7]
ma-hum-sey – *G. galeottiana* Baill. [3]
matambilla – *G. anomala* R.E.Fr. [3]
palo de chombo – *G. anomala* R.E.Fr. [3, 7]
palo de zope, palo de zopo – *G. anomala* R.E.Fr. [3, 7]
pusamat-kiui – *Guatteria* (Tot.) [3]
zope-zope – *G. anomala* R.E.Fr. [3]
zopo – *G. anomala* R.E.Fr. [7]

Panama
burillo – *G. allenii R.E.Fr.* [6]
malagueta, malagueto – *G. aeruginosa* Standl. [5]
malagueta prieto, malagueto prieto – *G. slateri* Standl. [5]

Peru
ag-guio – *Guatteria* [1]
anonia – *G. pleiocarpa* Diels [35]
anonilla – *Guatteria* [1]
auca hicoja – *Guatteriopsis blepharophylla* (Mart.) R.E. Fr. (=*Guatteriopsis sessiliflora* Benth. R.E.Fr.) [35]
cara huasca, carahuasca, carawasca, charahuaca, charahuasca, charahusca – *Guatteria* [1]; *G. chlorantha* Diels [21]; *G. elata* R.E.Fr. [24]; *G. phanerocampta* Diels [34]; *G. spectabilis* Diels [22]; *G. sp.* [21]
carahuasca bajo – *G. sp.* [21]
chuchuhuasca-mashan – *G. hyposericea* Diels [34]
enviha, envira – *Guatteria* [1]; *G. megalophylla* Diels [32]; *G. sp.* [21]
espinal – *G. modesta* Diels [34]
espintana – *G. citriodora* Ducke [24]; *G. modesta* Diels [22]
espintana negra – *Guatteria* [1]
espintanal – *Guatteria* [1]; *G. chlorantha* Diels [21]
hicoja negra – *G. macrocarpa* R.E.Fr. [35]
icoja, icoje – *Guatteria* [1]
jana huasca, janahuasco, yana huasca, yana waska – *Guatteria* [1]; *G. chlorantha* Diels [21, 22]; *G. hyposericea* Diels [34]; *G. sp.* [21]
paschaco – *G. chlorantha* Diels [21]
turtuga – *G. chlorantha* Diels [21]
tortuga caspi – *Guatteria* [1]; *G. microcarpa* Ruiz & Pav. [34]
yúno – *G. chlorantha* Diels [22]; *Guatteria* [1]
zorro caspi – *G. sp.* [52]

Puerto Rico
haya – *G. blainii* (Griseb.) Urb. [5]
haya blanca – *G. caribaea* Urb. [20]
haya minga – *G. blainii* (Griseb.) Urb. [5]
negra lora – *G. blainii* (Griseb.) Urb. [5]
ya ya – *G. caribaea* Urb. [20]

Salvador
flor de Guineo – *Guatteria* [1]

Suriname
arara – *G. sp.* (Ara.) [27]; *G. schomburgkiana* Mart. (Ara.) [44]
araraballi – *G. schomburgkiana* Mart. (Ara.) [27]
aremenango wewe/aremenango wéwé – *G. schomburgkiana* Mart. (Car.) [27, 44]
baaha koengé, baahaan koengé, baakakungè – *G. schomburgkiana* Mart. (Sar.) [27, 44]
baaka pau – *G. punctata* (Aubl.) R.A.Howard (Sar.) [van Andel, T.R., pers. comm.]
boesi-soensaka – *G. chrysopetala* (Steud.) (Sur.) [41]
bosolijf – *G. scandens* Ducke (Sur.) [27]
boszuurzak, boschzuurzak – *G. punctata* (Aubl.) R.A.Howard (Sur.) [27]; *G. schomburgkiana* Mart. (Sur.) [44]
busisunsaka – *G. schomburgkiana* Mart. (Sra.) [27]
djirikawa – *G. conspicua* R.E.Fr. (Ara.) [26]
jaro jaro – *G. schomburgkiana* Mart. (Car.) [44]
kasalerodañ – *G. scandens* Ducke (Ara.) [27]
kirikawa – *G. conspicua* R.E.Fr. (Ara.) [27]
koeliki kojoko karau bandihoro, korikie kojoko kazau bandihore, kurihi koyoko karau bandikoro – *G. schomburgkiana* Mart. (Ara.) [27, 44]
kofibali, kufiballi – *G. scandens* Ducke (Sur., Ara.) [27, 41]
krukurutitei – *G. schomburgkiana* Mart. (Sra.) [27]
kurihi koyoko – *G. schomburgkiana* Mart. (Ara.) [27]
kurihi koyoko ferobero – *G. schomburgkiana* Mart. (Ara.) [27]
kwiengé – *G. schomburgkiana* Mart. (Sar.) [27]
maboballi wadilikoro – *G. schomburgkiana* Mart. (Ara.) [27, 44]
mamaai – *G. punctata* (Aubl.) R.A.Howard (Sar.) [van Andel, T.R., pers. comm.]
moerewa – *G. scandens* Ducke (Car.) [44]
olijf – *G. scandens* Ducke (Sur.) [41]
olijfrank – *G. scandens* Ducke (Sur.) [44]
panta – *G. wachenheimii* Benoist (=*G. microsperma* R.E.Fr.) [26]
pajoelerian, pajoerian, payuriran, payuri-rang – *G. schomburgkiana* Mart. (Car.) [27, 44]
pegrekoe, pegreku – *G. schomburgkiana* Mart. (Sra.) [27, 44]
sabana pegrekoe, savanne pegreku – *G. schomburgkiana* Mart. (Sra.) [27, 44]
wajoeli – *G. schomburgkiana* Mart. (Car.) [44]
yariyari – *G. conspicua* R.E.Fr. (Sra.) [27]
yaroyaro – *G. schomburgkiana* Mart. (Car., Ara.?) [27]

Venezuela
laurel majagüillo – *G.* metensis R.E.Fr. [37]
malagueto – *G. rigidipes* R.E.Fr. [42]
ya ya – *G. schomburgkiana* Mart. [47]; *Guatteria* [1]
yalla – *Guatteria* [1]

VERNACULAR NAME REFERENCES

1. **Record, S.J. & Hess, R.W.** 1943. *Timbers of the New World*. Yale University Press, New Haven.
2. **Ortega, A.** 1976. Plantas del Ecuador: árboles de Morona. *Ciencia y Naturaleza* 17: 16-17.
3. **Martinez, M.** 1979. *Catálogo de nombres vulgares y científicos de plantas mexicanas*. Fondo de Cultura Económica, México.
4. **Pennington, T.D., Reynel, C. & Daza, A.** 2004. *Illustrated guide to the trees of Peru*. David Hunt, Sherborne, England.
5. **Bärner, J.** 1962. *Die Nutzhölzer der Welt*. Verlag von J. Cramer, Weinheim.
6. **Doyle, J.J. & al.** 1997. A phylogeny of the chloroplast gene *rbcL* in the Leguminosae: taxonomic correlations and insights into the evolution of nodulation. *Amer. J. Bot.* 84: 541-554.
7. **Pennington, T.D. & Sarukhán, J.** 1998. *Árboles tropicales de Mexico*. Universidad Nacional Autónoma de México, Fondo de Cultura Económica, México.
8. **Murillo-A., J. & Restrepo, D.** 2000. *Las Anonaceas de la region Araracuara*. Tropenbos Colombia, Colombia.
9. **Fanshawe, D.B.** 1949. *Check-list of the indigenous woody plants of British Guiana*. Forest Bull., Georgetown, n.s.
10. **Sandwith, N.Y.** 1930. Contributions to the flora of tropical America III. *Annonaceae* collected by the Oxford University Expedition to British Guiana, 1929. *Kew Bull.* 1930: 466-480.
11. **Klein, R.M.** 1969. Árvores nativas da Ilha de Santa Catarina. *Insula* 3: 9-10.
12. **Corréa, M.P.** 1931/1969/1974. *Diccionario das plantas uteis do Brasil e das exoticas cultivadas*. Imprensa Nacional, Rio de Janeiro.
13. **Fries, R.E.** 1927. Die von Ekman in Westindien gesammelten Annonaceen. *Ark. Bot.* 21A: 1-25.
14. **Bisse, J.** 1988. *Arboles de Cuba*. Editorial Cientifico-Técnica, Ciudad de la Habana.
15. **Barker, H.D. & Dardeau** 1930. *La flore d'Haiti*. Port-au-Prince, Haiti.
16. **Liogier, A.H.** 1983. *La flora de la Española, II*. Ediciones de la UCE, San Pedro de Macorís, R.D.
17. **Barrera, T.E.** 1985. Identificación de plàntulas de algunas especies arbóreas del bosque Niebla. *Perez-Arbelaezia* 1: 52.
18. **Whittall, J.B. & al.** 2006. Generating single-copy nuclear gene data for a recent adaptive radiation. *Mol. Phyl. Evol.* 39: 124-134.
19. **Fournet, J.** 1978. *Flore illustrée des phanérogames de Guadeloupe et de Martinique*. Inst. Nat. Rech. Agron., Paris.
20. **Liogier, A.H. & Martorell, L.F.** 1982. *Flora of Puerto Rico and adjacent islands. A systematic synopsis*. Editorial de la Universidad, Puerto Rico.
21. **Lebacq, L.** 1973. Classification de bios de l'Amazonie péruviene. *Mus. Roy. Afr. Centr., Doc. Econ.* 3: 68-69.
22. **Diels, L.** 1924. In: Mildbread, J. - Plantae Tessmannianae peruvianae 1. *Notizbl. Bot. Gart. Berlin-Dahlem* 9: 137-141.
23. **Porto, P.C.** 1936. Plantas indigenas e exoticas provenientes da Amazonônia, cultivadas no Jardin Botanico do Rio de Janeiro. *Rodriguésia* 2: 105-107.
24. **Encarnación, C.F.** 1983. *Nomenclatura de las especies forestales comunes en el Peru*. Documento de trabajo No. 7 (PNUD/FAO), Lima.
25. **Angely, J.** 1969. *Flora analítica e fitogeográfica do estado de São Paulo*. Edições Phyton, São Paulo.
26. **Jansen-Jacobs, M.J.** 1976. Annonaceae. In, *Pulle, A.A. - Flora of Suriname (Additions and corrections).* vol. 2, 2: 658-687. E.J. Brill., Leiden.
27. **Klooster, C.I.E.A. van 't , Lindeman, J.C. & Jansen-Jacobs, M.J.** 2003. Index of vernacular plant names of Suriname. *Blumea* Supplement 15: 1-322.
28. **da Silva, M.F.** 1977. *Nomes vulgares de plantas amazônicas*. INPA, Manaus.
29. **Grenand, P. & al.** 2004. *Pharmacopées traditionnelles en Guyane (Créoles, Wayãpi, Paikur)*. Institute de recherche pour le dévelopment, Paris.
30. **Reitz, R. & al.** 1978. Projeto madeira de Santa Catarina. *Sellowiana* 28-30: 20.
31. **van Andel, T.** 2000. *Non-timber forest products of the North-West District of Guyana. Part II: a field guide.* Tropenbos-Guyana Programme, Georgetown, Guyana.
32. **Fries, R.E.** 1934. Revision der Arten einiger Anonaceen-Gattungen III. *Acta Horti Berg.* 12: 1-220.
33. **Grenand, P. & al.** 1987. Pharmacopées traditionnelles en Guyane. *Mém. ORSTOM* 108: 97-111. 34. **Soukup, J.** 1962. Vocabulario de los nombres vulgares de la flora peruana. *Biota* 4: 228.
35. **Reisz, R.R. & Muller, J.** 2004. Molecular timescales and the fossil record: a paleontological perspective. *Trends Genet.* 20: 237-241.
36. **Peckolt, T.** 1897. Heil- und Nutzpflanzen Brasiliens aus der Familie der *Annonaceae*. *Ber. Deutsch. Pharm. Ges.* 7: 450-470.
37. **Steyermark, J.A. & Huber, O.** 1978. *Flora del Avila*. INCAFO, Madrid.
38. **Higuchi, N. & al.** 1985. Bacia 3 - Inventário florestal comerciál. *Acta Amazonica* 15: 358.
39. **Hohenkerk, L.S.** 1918. Botanical identification of British Guiana trees and plants. *J. Board Agric. British Guiana* 11: 99.
40. **Kuhlmann, M. & Kühn, E.** 1947. A flora do distrito de Ibiti. *Publ. da sér. "B", Inst. de Botânica, São Paulo* 60: 153-154.
41. **Roosmalen, M.G.M. van** 1987. Annonaceae. Pp. 4-20 in, *Fruits of the Guianan flora.*
42. **Ruiz-Teran, L.E. & Lopez-Palacios, S.** 1985. Notas etnobotanicas y nombres vulgares de plantas venezolanas. *Revista Fac. Far. (Merida)* 25: 5-95.
43. **Bremer, K.** 2000. Early Cretaceous lineages of monocot flowering plants. *Proc. Natl. Acad. Sci. USA* 97: 4707-4711.
44. **Fries, R.E.** 1940. in, *Pulle, A.A. - Flora of Suriname.*, vol. 2, part 2: 341-383.
45. **Glaziou, A.F.M.** 1905. Plantae Brasiliae centralis a Glaziou lectae. *Bull. Soc. Bot. France* 52, Mém. 3a: 10-11.

46. **Pontes, A.F., Barbosa, M.R.D.V. & Maas, P.J.M.** 2004. Flora Paraibana: Annonaceae Juss. *Acta bot. bras.* 18: 281-293.
47. **Pittier, H.** 1926. *Manual de las plantas usuales de Venezuela*. Litografía del Comercio, Caracas.
48. **Davis, E.W. & Yost, J.A.** 1983. The ethnodmedicine of the Waorani of Amazonian Ecuador. *J. Ethnopharm.* 9: 293.
49. **Braga, R.** 1960. *Plantas do Nordeste, especialmente do Ceará, ed. 2*. Imprensa oficial, Fortaleza (Ceará - Brazil).
50. **Emperaire, L.** 1983. *La caatinga du sud-est du Piauí (Brésil)*. Éditions recherche sur les civilisations, Paris.
51. **Anonymous** 1983. *Especies vegetales promisorias de los Países del Convenio "Andrés Bello"*. Editora Guidelupe Ltda., Bogotá.
52. **Nebel, G. & H. Meilby** 2005. Growth and population structure of timber species in Peruvian Amazon flood plains. *For. Ecol. Man.* 215: 196-211.

APPENDIX 1. TAXA, VOUCHER INFORMATION AND GENBANK/EBI ACCESSION NUMBERS OF DNA SEQUENCES.

Type specimens are indicated by an exclamation mark behind the herbarium acronym. Type specimens of species that have been synonymised are listed under their basionym, with the accepted species name in between brackets. If no Genbank/EBI accession number is listed, sequences were not or only partially obtained. UBG = Cultivated at the Utrecht University Botanical Garden.

Taxon	Geography	Voucher	UDNA	rbcL	trnLF	matK	psbA-trnH	ndhF	trnSG	atpB	trnTL	ncpGS
Anaxagorea phaeocarpa Mart.	Ecuador	Maas, P.J.M. 8592 (U)	498	AY238952	EF179316	AY238960	AY841426	EF179279	EF179321	EF179244	DQ861643	-----
Anaxagorea silvatica R.E.Fr.	Brazil	Maas, P.J.M. 8836 (U)	113	AY743439	AY743458	AY743477	AY841427	-----	EF179322	EF179245	DQ861644	-----
Annickia chlorantha (Oliv.) Setten & Maas	Gabon	Sosef, M.S.M. 1877 (WAG)	976	AY841594	AY841671	AY841393	AY841442	AY841401	AY841550	AY841370	AY841571	-----
Annickia pilosa (Exell) Setten & Maas	Gabon	Sosef, M.S.M. 1803 (WAG)	977	AY743450	AY743469	AY743488	AY841444	AY841402	AY841551	AY841371	AY841572	-----
Annona glabra L.	UBG (E83GR00360)	Chatrou, L.W. 467 (U)	522	AY841596	AY841673	DQ125050	DQ125116	EF179281	EF179323	EF179246	-----	-----
Annona muricata L.	UBG (83GR00169)	Chatrou, L.W. 468 (U)	525	AY743440	AY743459	AY743478	AY841428	EF179282	EF179324	EF179247	DQ861648	-----
Anonidium sp.	Cameroon	Cheek, M. 7896 (K)	38	AY841598	AY841675	DQ125051	DQ125117	EF179283	EF179325	EF179248	-----	-----
Artabotrys hexapetalus (L.f.) Bhandari	UBG (94GR01614)	Chatrou, L.W. 470 (U)	529	AY238953	EF179317	AY238962	AY841429	EF179284	EF179326	EF179249	DQ861649	-----
Artabotrys sp.	Gabon	Wieringa, J.J. 4018 (WAG)	121	AY841599	AY841676	DQ125052	DQ125118	EF179285	EF179327	EF179250	-----	-----
Asimina angustifolia A.Gray	USA	Weerasooriya, A. s.n. (MISS)	1076	DQ124939	AY841677	DQ125053	DQ125119	EF179286	EF179328	EF179251	-----	-----
Asimina triloba (L.) Dunal	UBG	Chatrou, L.W. 276 (U)	517	AY743441	AY743460	AY743479	AY841430	EF179287	EF179329	EF179252	-----	-----
Cleistopholis glauca Engl. & Diels	Gabon	Wieringa, J.J. 3278 (WAG)	198	AY841603	AY841681	AY841395	AY841432	AY841404	AY841549	AY841373	DQ861645	-----
Cremastosperma cauliflorum R.E.Fr.	Peru	Chatrou, L.W. 224 (U)	312	AY743519	AY743565	AY743542	AY841448	AY841406	AY841553	AY841375	AY841574	-----
Cyathocalyx martabanicus Hook.f. & Thoms.	Kabun Raya Bogor	Mols, J.B. 11 (L)	1002	AY841605	AY841683	DQ125054	DQ125120	EF179288	EF179330	EF179253	-----	-----
Cymbopetalum brasiliense (Vell.) Benth. ex Baill.	UBG (84GR00275)	Chatrou, L.W. 471 (U)	530	AY841608	AY841686	DQ125055	DQ125121	EF179289	EF179331	EF179254	DQ861646	-----
Dasymaschalon macrocalyx Finet & Gagnep.	Thailand	Kessler, P.J.A. 3199 (L)	997	AY841610	AY841688	EF179277	EF179313	EF179290	EF179332	EF179255	-----	-----
Diclinanona tessmannii Diels	Peru	Maas, P.J.M. 8198 (U)	76	AY841611	AY841689	DQ125056	EF179314	EF179291	EF179333	EF179256	-----	-----
Disepalum platypetalum Merr.	Indonesia	Takeuchi 18201 (?)	1077	AY841612	AY841690	DQ125057	DQ125122	EF179292	EF179334	EF179257	-----	-----
Duguetia hadrantha (Diels) R.E.Fr.	Peru	Chatrou, L.W. 181 (U)	288	AY738161	AY740573	AY740541	DQ125123	EF179293	EF179335	EF179258	DQ861650	-----
Duguetia sooretamae Maas	Brazil	Maas, P.J.M. 8827 (U)	428	AY738177	AY740589	AY740557	DQ861746	-----	-----	-----	DQ861651	-----
Duguetia staudtii (Engl. & Diels) Chatrou	Cameroon	Andel, T.R. van 3290 (U)	854	AY738178	AY740590	AY740558	DQ125124	EF179294	EF179336	EF179259	-----	-----
Fusaea peruviana R.E.Fr.	Peru	Chatrou, L.W. 179 (U)	287	AY743445	AY743464	AY743483	AY841436	EF179295	EF179337	EF179260	DQ861652	-----

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Goniothalamus griffithii Hook.f. & Thoms.	Thailand	Kessler, P.J.A. 3188 (L)	1019	AY743446	AY743465	AY743484	DQ125125	EF179296	EF179338	EF179261	-----	-----
Goniothalamus tapis Miq.	Thailand	Kessler, P.J.A. 3193 (L)	1017	AY841622	AY841700	DQ125058	DQ125126	EF179297	EF179339	EF179262	-----	-----
Guatteria aberrans Erkens & Maas	Panama	Maas, P.J.M. 9570 (U!)	1321	DQ124987	DQ125045	DQ125111	DQ125227	-----	-----	-----	-----	-----
Guatteria aeruginosa Standl.	Costa Rica	Chatrou, L.W. 66 (U)	221	AY740958	AY741007	AY740909	DQ125136	EF179299	EF179341	EF179264	DQ861661	-----
Guatteria alata Maas & Setten	Panama	Mori, S.A. 2894 (U)	776	AY740959	AY741008	AY740910	DQ125137	-----	-----	-----	-----	-----
Guatteria allenii R.E.Fr.	Panama	Maas, P.J.M. 9538 (U)	1348	DQ861791	DQ861843	DQ861697	DQ861747	-----	-----	-----	DQ861695	-----
Guatteria allenii R.E.Fr.	Panama	Mori, S.A. 2952 (U)	777	AY740960	AY741009	AY740911	DQ125138	-----	-----	-----	-----	-----
Guatteria alta R.E.Fr.	Colombia	Gentry, A.H. b48250 (U)	841	DQ124941	DQ124999	DQ125065	DQ125139	-----	-----	-----	-----	-----
Guatteria alutacea Diels	Bolivia	Chatrou, L.W. 339 (U)	578	AY740961	AY741010	AY740912	DQ125140	-----	-----	-----	DQ861682	-----
Guatteria amplifolia Triana & Planch.	Panama	Maas, P.J.M. 9574 (U)	1403	-----	-----	-----	EF179241	-----	-----	-----	-----	EF179231
Guatteria amplifolia Triana & Planch.	Panama	Maas, P.J.M. 9533 (U)	1400	-----	-----	-----	EF179238	-----	-----	-----	-----	EF179228
Guatteria amplifolia Triana & Planch.	Costa Rica	Maas, P.J.M. 9479 (U)	1399	-----	-----	-----	EF179237	-----	-----	-----	-----	EF179227
Guatteria amplifolia Triana & Planch.	Costa Rica	Maas, P.J.M. 9498 (U)	1398	-----	-----	-----	EF179236	-----	-----	-----	-----	EF179226
Guatteria amplifolia Triana & Planch.	Costa Rica	Chatrou, L.W. 111 (U)	252	DQ124942	DQ125000	DQ125066	DQ125141	-----	-----	-----	DQ861664	EF179222
Guatteria amplifolia Triana & Planch.	Belize	Holst, K. 4207 (U)	1422	-----	-----	-----	-----	-----	-----	-----	-----	-----
Guatteria anomala R.E.Fr.	Mexico	Ishiki, M. 2233 (U)	150	AY740962	AY741011	AY740913	AY841437	EF179298	EF179340	EF179263	DQ861657	EF179217
Guatteria anthracina Scharf & Maas	French Guiana	Scharf, U. 87 (U)	677	DQ861792	DQ861844	DQ861698	DQ861748	-----	-----	-----	-----	-----
Guatteria atra Sandwith aff.	Guyana	Gopaul, D. 2791 (U)	715	AY740963	AY741012	AY740914	DQ125142	-----	-----	-----	-----	-----
Guatteria australis A.St.-Hil. aff.	Brazil	Lobão, A.Q. 499 (U)	512	AY740964	AY741013	AY740915	AY841438	-----	-----	-----	DQ861675	-----
Guatteria blainii (Griseb.) Urb.	Dominican Republic	Maas, P.J.M. 6443 (U)	785	AY740965	AY741014	AY740916	DQ125143	-----	-----	-----	-----	-----
Guatteria blainii (Griseb.) Urb.	Cuba	Rainer, H. 1620 (WU)	1416	DQ861793	DQ861845	DQ861699	-----	-----	-----	-----	DQ861688	-----
Guatteria boliviana H.Winkl.	Bolivia	Solomon, J.C. 10789 (U)	838	DQ124943	DQ125001	DQ125067	DQ125144	-----	-----	-----	-----	-----
Guatteria boliviana H.Winkl.	Peru	Pirie, M.D. 120 (U)	1180	DQ861794	DQ861846	DQ861700	DQ861749	-----	-----	-----	-----	-----
Guatteria brevicuspis R.E.Fr.	Brazil	Prance, G.T. 16328 (U)	801	AY740966	AY741015	AY740917	DQ125145	-----	-----	-----	-----	-----
Guatteria brevipedicellata R.E.Fr.	Colombia	Lawrance, G.E. 771 (S!)	925	DQ124944	DQ125002	DQ125068	DQ125146	-----	-----	-----	-----	-----
Guatteria burchellii R.E.Fr.	Brazil	Carvalho, A.M. de 661 (U)	799	DQ861795	DQ861847	DQ861701	-----	-----	-----	-----	-----	-----
Guatteria caribaea Urb.	Dominican Republic	Tuxill, J. 89 (U)	786	AY740967	AY741016	AY740918	DQ125149	-----	-----	-----	DQ861689	-----
Guatteria cf *amplifolia* Triana & Planch.	Panama	Maas, P.J.M. 9549 (U)	1402	-----	-----	-----	EF179240	-----	-----	-----	-----	EF179230
Guatteria cf *amplifolia* Triana & Planch.	Panama	Maas, P.J.M. 9534 (U)	1401	-----	-----	-----	EF179239	-----	-----	-----	-----	EF179229
Guatteria cf *amplifolia* Triana & Planch.	Costa Rica	Maas, P.J.M. 9419 (U)	1397	-----	-----	-----	EF179235	-----	-----	-----	-----	EF179225
Guatteria cf *candolleana* Schltdl.	Brazil	Harley, R.M. 17360 (U)	798	DQ124946	DQ125004	DQ125070	DQ125148	-----	-----	-----	-----	-----
Guatteria cf *hilariana* Schltdl.	Brazil	Gottsberger, G.K. s.n. (U)	793	DQ124952	DQ125010	DQ125076	DQ125165	-----	-----	-----	-----	-----
Guatteria cf *lasiocalyx* R.E.Fr.	Brazil	Maas, P.J.M. 9000 (U)	549	DQ124969	DQ125027	DQ125093	DQ125202	-----	-----	-----	-----	-----
Guatteria cf *lasiocalyx* R.E.Fr.	Bolivia	Krukoff, B.A. 11086 (U)	839	DQ124945	DQ125003	DQ125069	DQ125147	-----	-----	-----	-----	-----
Guatteria cf *lucens* Standley	Costa Rica	Gómez, L.D. 23305 (U)	782	DQ124954	DQ125012	DQ125078	DQ125173	-----	-----	-----	-----	-----
Guatteria cf *meliodora* R.E.Fr.	Brazil	Maas, P.J.M. 9231 (U)	555	DQ124955	DQ125013	DQ125079	DQ125177	-----	-----	-----	DQ861677	-----

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Guatteria cf *pilosula* Planch. & Linden ex Triana & Planch.	Venezuela	Stergios, B. 20975 (U)	1418	DQ861813	DQ861866	DQ861717	DQ861763	-----	-----	-----	-----	-----
Guatteria chiriquiensis R.E.Fr.	Costa Rica	Chatrou, L.W. 43 (U)	202	AY740968	AY741017	AY740919	DQ125150	-----	-----	-----	-----	-----
Guatteria citriodora Ducke	Brazil	Ribeiro, J.E.L.S. 964 (U)	797	DQ861796	DQ861848	DQ861702	-----	-----	-----	-----	-----	-----
Guatteria costaricensis R.E.Fr.	Costa Rica	Maas, P.J.M. 9399 (U)	1338	-----	-----	-----	EF179234	-----	-----	-----	-----	EF179224
Guatteria curvinervia R.E.Fr.	Brazil	Gottsberger, G.K. (U)	796	DQ861797	DQ861849	-----	-----	-----	-----	-----	-----	-----
Guatteria decurrens R.E.Fr.	Peru	Maas, P.J.M. 8314 (U)	834	DQ861798	DQ861850	DQ861703	-----	-----	-----	-----	-----	-----
Guatteria diospyroides Baill.	Nicaragua	Stevens, W.D. 4946 (U)	1421	-----	-----	-----	EF179243	-----	-----	-----	-----	EF179233
Guatteria diospyroides Baill.	Costa Rica	Chatrou, L.W. 84 (U)	233	AY740969	AY741018	AY740920	DQ125152	-----	-----	-----	-----	EF179221
Guatteria diospyroides Baill.	Mexico	Davidse, G. 20398 (U)	1420	-----	-----	-----	EF179242	-----	-----	-----	-----	EF179232
Guatteria discolor R.E.Fr. aff.	Brazil	Maas, P.J.M. 9030 (U)	552	AY740970	AY741019	AY740921	DQ125153	-----	-----	-----	DQ861676	-----
Guatteria dolichopoda Donn.Sm.	Costa Rica	Maas, P.J.M. 9484 (U)	1345	DQ861800	DQ861852	DQ861704	DQ861751	-----	-----	-----	DQ861693	-----
Guatteria dolichopoda Donn.Sm.	Panama	Maas, P.J.M. 9508 (U)	1346	DQ861801	DQ861853	DQ861705	DQ861752	-----	-----	-----	DQ861694	-----
Guatteria dumetorum R.E.Fr.	Panama	Maas, P.J.M. 9581 (U)	1350	DQ861799	DQ861851	-----	DQ861750	-----	-----	-----	-----	-----
Guatteria dumetorum R.E.Fr.	Panama	FLORPAN 2497 (U)	779	AY740971	AY741020	AY740922	DQ125154	-----	-----	-----	-----	-----
Guatteria ecuadorensis R.E.Fr.	Ecuador	Mexia, Y. 711 (S!)	914	DQ861802	DQ861854	DQ861706	DQ861753	-----	-----	-----	-----	-----
Guatteria elegantissima R.E.Fr.	Colombia	Gentry, A.H. 56948 (U)	833	AY740973	AY741022	AY740924	DQ125157	-----	-----	-----	-----	-----
Guatteria excellens R.E.Fr.	Peru	Díaz, P. 85 (U)	832	DQ861803	DQ861855	DQ861707	DQ861754	-----	-----	-----	-----	-----
Guatteria ferruginea A.St.-Hil.	Brazil	Lobão, A.Q. 643 (U)	565	DQ124949	DQ125007	DQ125073	DQ125158	-----	-----	-----	-----	-----
Guatteria galeottiana Baill.	Mexico	Beaman, J.H. 6121 (U)	1404	DQ124950	DQ125008	DQ125074	DQ125160	-----	-----	-----	-----	-----
Guatteria glabrescens R.E.Fr.	Brazil	Maas, P.J.M. 8816 (U)	99	AY740975	AY741024	AY740926	DQ125161	EF179300	EF179342	EF179265	DQ861656	-----
Guatteria gracilipes R.E.Fr.	Brazil	Krukoff, B.A. 1156 (S!)	910	DQ124951	DQ125009	DQ125075	DQ125162	-----	-----	-----	-----	-----
Guatteria heterotricha R.E.Fr.	Colombia	Monsalve B., M. 1262 (U)	829	AY740977	AY741026	AY740928	DQ125164	-----	-----	-----	-----	-----
Guatteria hilariana var. *verruculosa* Schltdl.	Brazil	Mosén, C.W.H. 3337 (S!)	909	DQ861806	DQ861858	DQ861710	DQ861756	-----	-----	-----	-----	-----
Guatteria hyposericea Diels aff.	Bolivia	Chatrou, L.W. 375 (U)	580	AY740978	AY741027	AY740929	DQ125166	-----	-----	-----	DQ861683	-----
Guatteria guianensis (Aubl.) R.E.Fr.	Brazil	Webber, A.C. 1884 (U)	560	AY740976	AY741025	AY740927	DQ125163	-----	-----	-----	DQ861678	-----
Guatteria foliosa Benth.	Bolivia	Chatrou, L.W. 325 (U)	575	AY740974	AY741023	AY740925	DQ125159	-----	-----	-----	DQ861681	-----
Guatteria modesta Diels	Colombia	Dulmen, A. van 183 (U)	823	DQ124957	DQ125015	DQ125081	DQ125179	-----	-----	-----	-----	-----
Guatteria dusenii R.E.Fr.	Brazil	Dusén, P. 13752 (S!)	915	DQ124948	DQ125006	DQ125072	DQ125155	-----	-----	-----	-----	-----
Guatteria elata R.E.Fr.	Peru	Chatrou, L.W. 252 (U)	328	AY740972	AY741021	AY740923	DQ125156	-----	-----	-----	DQ861671	-----
Guatteria neglecta R.E.Fr.	Brazil	Gottsberger, G.K. (U)	787	DQ861810	DQ861862	DQ861713	DQ861759	-----	-----	-----	-----	-----
Guatteria olivacea R.E.Fr.	Peru	Chatrou, L.W. 209 (U)	304	AY740989	AY741038	AY740940	DQ125183	-----	-----	-----	DQ861669	-----
Guatteria inuncta R.E.Fr.	Costa Rica	Liesner, R.L. 14631 (U)	780	AY740979	AY741028	AY740930	DQ125167	-----	-----	-----	-----	EF179223
Guatteria inundata Mart.	Peru	Chatrou, L.W. 191 (U)	291	AY740980	AY741029	AY740931	DQ125168	-----	-----	-----	DQ861668	-----
Guatteria jefensis Barringer	Panama	Valdespino, I.A. 685 (U)	781	AY740981	AY741030	AY740932	DQ125169	-----	-----	-----	-----	-----
Guatteria jefensis Barringer	Panama	Maas, P.J.M. 9553 (U)	1349	DQ861805	DQ861857	DQ861709	DQ861755	-----	-----	-----	-----	-----
Guatteria juruensis Diels	Peru	Asplund, E. 14440 (U)	1413	DQ861804	DQ861856	DQ861708	-----	-----	-----	-----	-----	-----
Guatteria latifolia (Mart.) R.E.Fr.	Brazil	Lobão, A.Q. 544 (U)	510	AY740982	AY741031	AY740933	DQ125170	-----	-----	-----	DQ861673	EF179219

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Guatteria latisepala R.E.Fr.	Colombia	Sánchez, D. 404 (U)	827	DQ124953	DQ125011	DQ125077	DQ125171	-----	-----	-----	-----	-----
Guatteria lehmannii R.E.Fr.	Colombia	Cuatrecasas, J. 22297 (S!)	931	DQ861807	DQ861859	DQ861711	DQ861757	-----	-----	-----	-----	-----
Guatteria liesneri D.M. Johnson & N.A. Murray	Brazil	Cid F., C.A. 8403 (U)	792	AY740983	AY741032	AY740934	DQ125172	-----	-----	-----	-----	-----
Guatteria liesneri D.M. Johnson & N.A. Murray	Venezuela	Kral, R. 71950 (U)	826	DQ861808	DQ861860	-----	-----	-----	-----	-----	-----	-----
Guatteria macropus Mart.	Brazil	Pirani, J.R. 2725 (U)	790	AY740984	AY741033	AY740935	DQ125174	-----	-----	-----	-----	-----
Guatteria maypurensis Kunth	Guyana	Jansen-Jacobs, M.J. 5416 (U)	182	AY740985	AY741034	AY740936	DQ125175	-----	-----	-----	-----	-----
Guatteria megalophylla Diels	Peru	Chatrou, L.W. 216 (U)	309	AY740986	AY741035	AY740937	DQ125176	-----	-----	-----	-----	-----
Guatteria mexiae R.E.Fr.	Brazil	Mori, S.A. 9722 (U)	789	DQ124956	DQ125014	DQ125080	DQ125178	-----	-----	-----	-----	-----
Guatteria moralesii (M. Gómez) Urb.	Cuba	Wright, C. 1851 (S!)	904	DQ861809	DQ861861	DQ861712	DQ861758	-----	-----	-----	-----	-----
Guatteria multivenia Diels	Ecuador	Maas, P.J.M. 8611 (U)	822	AY740987	AY741036	AY740938	DQ125180	-----	-----	-----	-----	-----
Guatteria notabilis Mello-Silva & Pirani	Brazil	Lobão, A.Q. 623 (U)	567	DQ124958	DQ125016	DQ125082	DQ125181	-----	-----	-----	DQ861680	-----
Guatteria notabilis Mello-Silva & Pirani	Brazil	Irwin, H.S. 27980 (U)	812	DQ861811	DQ861863	DQ861714	DQ861760	-----	-----	-----	-----	-----
Guatteria oligocarpa Mart.	Brazil	Maas, P.J.M. 7006 (U)	811	AY740988	AY741037	AY740939	DQ125182	-----	-----	-----	-----	-----
Guatteria oliviformis Donn.Smith	Costa Rica	Chatrou, L.W. 80 (U)	230	AY740990	AY741039	AY740941	DQ125184	-----	-----	-----	DQ861662	-----
Guatteria ouregou (Aubl.) Dunal	French Guiana	Scharf, U. 85 (U)	679	AY740991	AY741040	AY740942	DQ125185	-----	-----	-----	-----	-----
Guatteria ovalifolia R.E.Fr.	Guyana	Scharf, U. 34 (U)	687	DQ861812	DQ861864	DQ861715	DQ861761	-----	-----	-----	-----	-----
Guatteria pacifica R.E.Fr.	Colombia	Gentry, A.H. 62881 (U)	821	DQ124959	DQ125017	DQ125083	DQ125186	-----	-----	-----	-----	-----
Guatteria pacifica R.E.Fr.	Colombia	Cuatrecasas, J. 17150 (S!)	887	DQ124960	DQ125018	DQ125084	DQ125187	-----	-----	-----	-----	-----
Guatteria paraensis R.E.Fr.	Brazil	Fróes, R. 1753 (U)	810	DQ124961	DQ125019	DQ125085	DQ125188	-----	-----	-----	-----	-----
Guatteria parvifolia R.E.Fr.	Brazil	Gottsberger, G.K. 573007 (U)	809	AY740992	AY741041	AY740943	DQ125189	-----	-----	-----	-----	-----
Guatteria parvifolia R.E.Fr.	Brazil	Hoehne, F.C. SP28405 (S!)	889	-----	DQ861865	DQ861716	DQ861762	-----	-----	-----	-----	-----
Guatteria pittieri R.E.Fr.	Colombia	Werff, H. van der 9767 (U)	819	AY740993	AY741042	AY740944	DQ125190	-----	-----	-----	-----	-----
Guatteria poeppigiana Mart.	Brazil	Prance, G.T. 1775 (U)	808	DQ124962	DQ125020	DQ125086	DQ125191	-----	-----	-----	-----	-----
Guatteria pogonopus Mart.	Brazil	Kollmann, L. 202 (U)	807	DQ124963	DQ125021	DQ125087	DQ125192	-----	-----	-----	-----	-----
Guatteria pohliana Schltdl.	Brazil	Anderson, W.R. 35703 (U)	806	DQ124964	DQ125022	DQ125088	DQ125193	-----	-----	-----	-----	-----
Guatteria polyantha R.E.Fr.	Brazil	Costa, R.C.M. 284 (S!)	890	DQ124965	DQ125023	DQ125089	DQ125194	-----	-----	-----	-----	-----
Guatteria polycarpa R.E.Fr.	Brazil	Dusén, P. 7414 (S!)	891	DQ124966	DQ125024	DQ125090	DQ125195	-----	-----	-----	-----	-----
Guatteria pubens (Mart.) R.E.Fr.	Brazil	Spada, J. 198 (U)	805	DQ124967	DQ125025	DQ125091	DQ125196	-----	-----	-----	-----	-----
Guatteria pudica N.Zamora & Maas	Costa Rica	Chatrou, L.W. 107 (U)	249	AY740994	AY741043	AY740945	DQ125197	-----	-----	-----	DQ861663	-----
Guatteria punctata (Aubl.) R.A. Howard	French Guiana	Molino, J.F. 1593 (U)	482	AY740995	AY741044	AY740946	DQ125198	-----	-----	-----	DQ861672	-----
Guatteria puncticulata R.E.Fr.	Peru	Chatrou, L.W. 172 (U)	283	AY740996	AY741045	AY740947	DQ125199	-----	-----	-----	DQ861666	-----
Guatteria recurvisepala R.E.Fr.	Costa Rica	Chatrou, L.W. 61 (U)	217	AY740997	AY741046	AY740948	DQ125200	-----	-----	-----	DQ861659	-----
Guatteria reflexa R.E.Fr.	Brazil	Glaziou, A.F.M. 5725 (S!)	893	DQ124968	DQ125026	DQ125092	DQ125201	-----	-----	-----	-----	-----
Guatteria rigida R.E.Fr.	Brazil	Irwin, H.S. 6670 (U)	804	DQ861814	DQ861867	DQ861718	-----	-----	-----	-----	-----	-----
Guatteria rigidipes R.E.Fr.	Costa Rica	Skutch, A.F. 2553 (S!)	896	DQ124970	DQ125028	DQ125094	DQ125203	-----	-----	-----	-----	-----
Guatteria riparia R.E.Fr.	Venezuela	Maguire, B. 34835 (K)	1395	DQ861815	DQ861868	DQ861719	DQ861764	-----	-----	-----	-----	-----
Guatteria rotundata Maas & Setten	Panama	Mori, S.A. 5531 (U)	783	AY740998	AY741047	AY740949	DQ125204	-----	-----	-----	DQ861687	-----
Guatteria rupestris Mello-Silva & Pirani	Brazil	Cordeiro, I., CFCR 4116 (U)	803	AY740999	AY741048	AY740950	DQ125205	-----	-----	-----	-----	-----

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Guatteria sabuletorum R.E.Fr.	Brazil	Ducke, A. RB19617 (S!)	869	DQ861817	DQ861870	DQ861721	DQ861766	-----	-----	-----	-----	-----
Guatteria saffordiana Pitt.	Venezuela	Hokche, O. 825 (U)	1419	DQ861816	DQ861869	DQ861720	DQ861765	-----	-----	-----	-----	-----
Guatteria scandens Ducke	Guyana	Jansen-Jacobs, M.J. 5494 (U)	183	DQ124971	DQ125029	DQ125095	DQ125207	-----	-----	-----	DQ861658	-----
Guatteria schlechtendaliana Mart.	Brazil	Kollmann, L. 871 (U)	802	DQ124972	DQ125030	DQ125096	DQ125208	-----	-----	-----	-----	-----
Guatteria schomburgkiana Mart.	Guyana	Scharf, U. 45 (U)	694	DQ861819	DQ861872	DQ861723	DQ861767	-----	-----	-----	-----	-----
Guatteria schomburgkiana Mart.	Guyana	Scharf, U. 60 (U)	696	AY741001	AY741050	AY740952	DQ125209	-----	-----	-----	DQ861686	-----
Guatteria schomburgkiana Mart.	Guyana	Scharf, U. 46 (U)	690	DQ861818	DQ861871	DQ861722	-----	-----	-----	-----	-----	-----
Guatteria schunkevigoi D.R.Simpson	Peru	Schunke V., J. 3551 (S!)	870	DQ124973	DQ125031	DQ125097	DQ125210	-----	-----	-----	-----	-----
Guatteria scytophylla Diels	Brazil	Maas, P.J.M. 6956 (U)	559	AY741002	AY741051	AY740953	DQ125211	-----	-----	-----	-----	-----
Guatteria sellowiana Schltdl. aff.	Brazil	Lobão, A.Q. 557 (U)	511	AY741003	AY741052	AY740954	DQ125212	-----	-----	-----	DQ861674	-----
Guatteria sessilicarpa Maas & Setten	Panama	Maas, P.J.M. 9554 (U)	1320	DQ124974	DQ125032	DQ125098	DQ125214	-----	-----	-----	DQ861692	-----
Guatteria sessilicarpa Maas & Setten	Panama	McPherson, G. 12599 (U)	784	AY741004	AY741053	AY740955	DQ125213	-----	-----	-----	-----	-----
Guatteria sessilis R.E.Fr.	Venezuela	Liesner, R.L. 8546 (U)	818	DQ124975	DQ125033	DQ125099	DQ125215	-----	-----	-----	-----	-----
Guatteria sordida var. *lancifolia* R.E.Fr.	Brazil	Riedel, L. 1689 (S!)	871	DQ861820	DQ861873	DQ861724	DQ861768	-----	-----	-----	-----	-----
Guatteria sordida var. *ovalis* R.E.Fr.	Brazil	Riedel, L. 1689 (S!)	872	DQ124976	DQ125034	DQ125100	DQ125216	-----	-----	-----	-----	-----
Guatteria sphaerantha R.E.Fr.	Colombia	Faber-Langendoen, D. 1556 (U)	817	DQ124977	DQ125035	DQ125101	DQ125217	-----	-----	-----	-----	-----
Guatteria stipitata R.E.Fr.	Peru	Jaramillo, N. 820 (U)	816	DQ124978	DQ125036	DQ125102	DQ125218	-----	-----	-----	-----	-----
Guatteria subsessilis Mart.	Bolivia	Maas, P.J.M. 8684 (U)	90	DQ124979	DQ125037	DQ125103	DQ125219	-----	-----	-----	DQ861655	-----
Guatteria talamancana Zamora & Maas	Panama	Maas, P.J.M. 9516 (U)	1319	DQ861825	DQ861878	DQ861729	DQ861773	-----	-----	-----	DQ861691	-----
Guatteria tomentosa R.E.Fr.	Peru	Schunke V., J. 14061 (U)	815	DQ124988	DQ125046	DQ125112	DQ125229	-----	-----	-----	-----	-----
Guatteria tomentosa R.E.Fr.	Panama	Maas, P.J.M. 9521 (U)	1386	DQ861826	DQ861879	DQ861730	DQ861774	-----	-----	-----	-----	-----
Guatteria tomentosa R.E.Fr. aff.	Panama	Maas, P.J.M. 9528 (U)	1387	DQ861823	DQ861876	DQ861727	DQ861771	-----	-----	-----	-----	-----
Guatteria tonduzii Diels	Costa Rica	Chatrou, L.W. 121 (U)	259	AY741005	AY741054	AY740956	DQ125228	-----	-----	-----	DQ861665	-----
Guatteria trichoclonia Diels	Bolivia	Buchtien, O. 698 (S!)	877	DQ861827	DQ861880	DQ861731	DQ861775	-----	-----	-----	-----	-----
Guatteria ucayaliana Hub.	Peru	Asplund, E. 12930 (U)	1412	DQ861828	DQ861881	DQ861732	DQ861776	-----	-----	-----	-----	-----
Guatteria velezii R.E.Fr. (= *G. maypurensis* Kunth)	Venezuela	Velez, I. 2488 (S!)	880	DQ861829	DQ861882	DQ861733	DQ861777	-----	-----	-----	-----	-----
Guatteria venezuelana R.E.Fr.	Venezuela	Meier, G.W. (U)	1417	DQ861831	DQ861884	DQ861735	DQ861779	-----	-----	-----	-----	-----
Guatteria venezuelana R.E.Fr.	Venezuela	Steyermark, J.A. 55097 (S!)	881	DQ861830	DQ861883	DQ861734	DQ861778	-----	-----	-----	-----	-----
Guatteria venezuelana R.E.Fr.	Venezuela	Wingfield, R. 6688 (U)	814	DQ124989	DQ125047	DQ125113	DQ125230	-----	-----	-----	-----	-----
Guatteria verruculosa R.E.Fr.	Colombia	Fosberg, F.R. 19126 (S!)	882	DQ124990	DQ125048	DQ125114	DQ125231	-----	-----	-----	DQ861690	-----
Guatteria villosissima A.St.-Hil.	Brazil	Lobão, A.Q. 630 (U)	564	AY741006	AY741055	AY740957	DQ125232	-----	-----	-----	DQ861679	-----
Guatteria wachenheimii Benoist	Guyana	Scharf, U. 43 (U)	689	DQ124991	DQ125049	DQ125115	DQ125233	-----	-----	-----	DQ861684	EF179218
Guatteria zamorae Erkens & Maas	Panama	Maas, P.J.M. 9531 (U!)	1347	DQ861832	DQ861885	DQ861736	DQ861780	-----	-----	-----	-----	-----
Guatteria sp.	Costa Rica	Chatrou, L.W. 65 (U)	220	DQ124947	DQ125005	DQ125071	DQ125151	-----	-----	-----	DQ861660	EF179220
Guatteria sp.	Peru	Pirie, M.D. 50 (U)	1125	DQ124985	DQ125043	DQ125109	DQ125225	-----	-----	-----	-----	-----
Guatteria sp.	Peru	Pirie, M.D. 158 (U)	1214	DQ861822	DQ861875	DQ861726	DQ861770	-----	-----	-----	-----	-----
Guatteria sp.	Brazil	Lobão, A.Q. 565 (U)	513	AY741000	AY741049	AY740951	DQ125206	-----	-----	-----	-----	-----
Guatteria sp.	Peru	Pirie, M.D. 143 (U)	1199	DQ124986	DQ125044	DQ125110	DQ125226	-----	-----	-----	-----	-----

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Guatteria sp.	Peru	Pirie, M.D. 130 (U)	1188	DQ861821	DQ861874	DQ861725	DQ861769	-----	-----	-----	-----	-----
Guatteria sp.	Guyana	Prévost M.-F. 4247 (U)	692	DQ124984	DQ125042	DQ125108	DQ125224	-----	-----	-----	DQ861685	-----
Guatteria sp.	Peru	Chatrou, L.W. 174 (U)	285	DQ124981	DQ125039	DQ125105	DQ125221	-----	-----	-----	DQ861667	-----
Guatteria sp.	Costa Rica	Chatrou, L.W. 118 (U)	256	DQ124980	DQ125038	DQ125104	DQ125220	-----	-----	-----	-----	-----
Guatteria sp. Section *Mecocarpus* R.E.Fr.	Peru	Chatrou, L.W. 196 (U)	295	DQ124982	DQ125040	DQ125106	DQ125222	-----	-----	-----	-----	-----
Guatteria sp. Section *Mecocarpus* R.E.Fr.	Bolivia	Chatrou, L.W. 463 (U)	593	DQ861824	DQ861877	DQ861728	DQ861772	-----	-----	-----	-----	-----
Guatteria sp. Section *Mecocarpus* R.E.Fr.	Peru	Chatrou, L.W. 245 (U)	323	DQ124983	DQ125041	DQ125107	DQ125223	-----	-----	-----	DQ861670	-----
Guatteriella tomentosa R.E.Fr.	Brazil	Daly, D.C. 4494 (U)	1405	DQ861833	DQ861886	DQ861737	DQ861781	-----	-----	-----	-----	-----
Guatteriopsis blepharophylla (Mart.) R.E. Fr.	Brazil	Prance, G.T. 25063 (K)	1389	DQ861835	DQ861888	DQ861739	DQ861783	-----	-----	-----	-----	-----
Guatteriopsis blepharophylla (Mart.) R.E. Fr.	French Guiana	Hahn, W.J. 3656 (U)	948	DQ861834	DQ861887	DQ861738	DQ861782	-----	-----	-----	-----	-----
Guatteriopsis friesiana W.A. Rodrigues	Brazil	Dick, C.W. 79 (K)	1391	DQ861836	DQ861889	DQ861740	DQ861784	-----	-----	-----	-----	-----
Guatteriopsis hispida R.E.Fr.	Brazil	Miralha, J.M.S. 295 (K)	1396	DQ861837	DQ861890	DQ861741	DQ861785	-----	-----	-----	-----	-----
Guatteriopsis kuhlmannii R.E.Fr.	Brazil	Pires, J.M. 50875 (U)	1406	DQ861838	DQ861891	DQ861742	DQ861786	-----	-----	-----	-----	-----
Guatteriopsis ramiflora D.R.Simpson	Peru	Schunke V., J. 8073 (U)	951	DQ124940	DQ124998	DQ125064	DQ125135	-----	-----	-----	-----	-----
Guatteriopsis ramiflora D.R.Simpson	Peru	Pirie, M.D. 23 (U)	1109	DQ861839	DQ861892	DQ861743	DQ861787	-----	-----	-----	-----	-----
Heteropetalum spruceanum R.E.Fr.	Brazil	Stevenson, D.W. 1115 (U)	942	DQ861840	DQ861893	DQ861744	DQ861788	-----	-----	-----	-----	-----
Heteropetalum spruceanum R.E.Fr.	Brazil	Kawasaki, M.L. 235 (K)	1392	DQ861841	DQ861894	DQ861745	DQ861789	-----	-----	-----	-----	-----
Isolona campanulata Engl. & Diels	UBG (86GR00240)	Chatrou, L.W. 472 (U)	531	AY238954	EF179318	AY238963	DQ125127	EF179301	EF179343	EF179266	-----	-----
Klarobelia inundata Chatrou	Peru	Chatrou, L.W. 205 (U)	301	AY743452	AY743471	AY743490	AY841469	AY841409	AY841556	AY841378	AY841577	-----
Letestudoxa bella Pellegr.	Gabon	Wieringa, J.J. 2797 (WAG)	145	AY841629	AY841707	DQ125059	DQ125128	EF179302	EF179344	EF179267	DQ861653	-----
Mkilua fragrans Verdc.	UBG (E91GR01649)	Chatrou, L.W. 474 (U)	1271	AY841634	AY841712	DQ125060	DQ861696	EF179303	EF179345	EF179268	DQ861647	-----
Monanthotaxis whytei (Stapf) Verdc.	UBG (84GR00388)	Chatrou, L.W. 475 (U)	533	AY841635	AY841713	EF179278	EF179315	EF179304	EF179346	EF179269	-----	-----
Monocarpia euneura Miq.	Indonesia	Slik, F. 2931 (L)	1407	AY318998	AY319111	AY518865	AY841477	AY841412	AY841559	AY841381	AY841580	-----
Monodora myristica (Gaertn.) Dunal	UBG (E84GR00389)	Chatrou, L.W. 477 (U)	535	AY743447	AY743466	AY743485	DQ125129	EF179305	EF179347	EF179270	-----	-----
Mosannona costaricensis R.E.Fr.	Costa Rica	Chatrou, L.W. 90 (U)	237	AY743510	AY743496	AY743503	AY841479	AY841413	AY841560	AY841382	AY841581	-----
Neostenanthera myristicifolia (Oliv.) Exell	Gabon	Wieringa, J.J. 3566 (WAG)	54	AY743448	AY743467	AY743486	DQ125130	EF179306	EF179348	EF179271	-----	-----
Piptostigma mortehani De Wild.	Gabon	Wieringa, J.J. 2779 (WAG)	505	AY743454	AY743473	AY743492	AY841498	AY841415	AY841562	AY841384	AY841583	-----
Pseudartabotrys letestui Pellegr.	Gabon	Wieringa, J.J. 3273 (WAG)	481	AY841650	AY841728	DQ125061	DQ125131	EF179307	EF179349	EF179272	-----	-----
Rollinia herzogii R.E.Fr.	Bolivia	Chatrou, L.W. 347 (U)	1051	AY841656	AY841734	DQ125062	DQ125132	EF179308	EF179350	EF179273	-----	-----
Sapranthus viridiflorus G.E.Schatz	Costa Rica	Chatrou, L.W. 55 (U)	211	AY319051	AY319165	AY743493	AY841515	AY841422	AY841569	AY841391	AY841590	-----
Trigynaea lanceipetala D.M.Johnson & N.A.Murray	Peru	Chatrou, L.W. 234 (U)	318	AY743449	AY743468	AY743487	-----	EF179309	EF179351	EF179274	-----	-----
Uvaria lucida Benth. subsp. virens (N.E.Br.) Verdc.	UBG,	BT 84GR00334 (U)	538	AY238957	EF179319	AY238966	AY841440	EF179310	EF179352	EF179275	-----	-----
Xylopia ferruginea Baill.	Indonesia	Slik, F. (L)	1010	AY841666	AY841744	DQ125063	DQ125133	EF179311	-----	-----	-----	-----
Xylopia peruviana R.E.Fr.	UBG (84GR00271)	Chatrou, L.W. 483 (U)	539	AY238958	EF179320	AY238967	DQ125134	EF179312	EF179353	EF179276	DQ861654	-----

APPENDIX 2: INDEX TO SPECIES AND INFRASPECIFIC TAXA OF *GUATTERIA*, *GUATTERIOPSIS*, *GUATTERIELLA* AND *HETEROPETALUM*

INTRODUCTION

A list of all published names of *Guatteria*, *Guatteriopsis*, *Guatteriella* and *Heteropetalum* on the species level and below is presented. Reference and year of first publication, synonymy and typification are mentioned. It also includes some nomina nuda. This list is mainly based on Maas' & al. (1994) index of Neotropical Annonaceae, but was extended with data from Annonbase (Rainer and Chatrou, 2006) and information collected by Erkens. Although *Guatteria* is a solely Neotropical genus, for the sake of clarity some entries for Paleotropical taxa are included in the main index. This occurs whenever the same name was published for a Neotropical as well as a paleotropical taxon. To be complete, a second index of all paleotropical names of *Guatteria* is also included. These Paleotropical entries were taken from Keßler & al. (1995) and are still provisional.

Although the present *Index* has been thoroughly checked, it may still contain various errors and omissions. Any comments and correction will therefore greatly be welcomed.

EXPLANATION OF THE INDEX

Each entry may be made up of three elements which are explained below:

1. Name and reference.

- Currently accepted names are printed in bold face. Names not printed as such are synonyms. Entries for nomina nuda, missapplied names, errors, or orthographic variants are placed between square brackets [ ].
- Author's names are abbreviated according to Brummitt and Powell's (1992) *Authors of Plant Names*.
- Titles of journals and periodicals are abbreviated in accordance with *Botonico-Periodicum-Huntianum* (Lawrence & al., 1968; Bridson and Smith, 1991). Titles of books and year of publication are listed as in *Taxonomic literature*, ed. 2 (Stafleu and Cowan, 1976-1987).
- Whenever applicable the reference is followed by:
    "nom. illeg.": an illegitimate name;
    "nom. nud.": a nomen nudem (invalidly published).

2. Type and type location.

For the type indication the following abbreviations are used:
HT: holotype;
IT: isotype;
LT: lectotype;
ST: syntype

T: type (used when the status of the type collection could not be determined yet; if this is followed by a blank space, the type collection could not be traced).
Type location is indicated by the herbarium acronym according to *Index Herbariorum* (Holmgren & al., 1990). Locations of isotypes are given as far as known.

3. Synonymy.
Nomenclatural synonyms are indicated by the symbol ≡ , and taxonomic synonyms by the symbol = . Non-annonaceous taxa are indicated by the proper name of the family placed between { }.

The foregoing may be illustrated by the next examples:

(1) **Guatteria aberrans** Erkens & Maas, Blumea 51(2): 201. f. 1. 2006.
(2) HT: Maas, P.J.M. 9570 (U); IT: INB, K, MO, PMA, SCZ.

(1) **Guatteria apodocarpa** Mart. in Mart., Fl. bras. 13(1): 30. 1841.
(2) HT: von Martius, C.F.P. s.n. (M).
(3) = **Rollinia parviflora** A. St.Hil.

(1) [Guatteria choroniensis Tamayo, Bol. Soc. Venez. Ci. Nat. 7(49): 210. 1942, nom. nud.]

(1) Guatteria berteriana Spreng., Syst. veg. 2: 635. 1825.
(2) T: Bertero s.n. (TO).
(3) = **Drypetes alba** Poit. (fide Urb., Symb. antill. 4: 340. 1905) {Euphorbiaceae}.

1. INDEX TO NEOTROPICAL NAMES

Guatteria aberemoa Dunal, Monogr. Anonac. 126. 1817, nom. illeg.
Aberemoa guianensis Aubl. (≡ **Guatteria guianensis** (Aubl.) R.E. Fr.).

Guatteria aberemoa Dunal var. microcarpa DC., Syst. nat. 1: 502. 1817.
T: ... (P?)
= **Guatteria guianensis** (Aubl.) R.E. Fr.

Guatteria aberrans Erkens & Maas, Blumea 51(2): 201. f. 1. 2006.
HT: Maas, P.J.M. 9570 (U); IT: INB, K, MO, PMA, SCZ.

Guatteria acrantha Erkens & Maas, Blumea 51(2): 202. t. 1; f. 2, 3. 2006.
HT: Rivera, N. 355 (SCZ); IT: PMA, U.

Guatteria acutiflora Dunal, Monogr. Anonac. 134. (1817). [Paleotropics]
T:
= **Polyalthia korinti** (Dunal) Thwaites.

[Guatteria acutiflora Wall., Cat. n. 6438. 1832, nom. nud.] [Paleotropics]
T:
= **Alphonsea zeylanica** J.D. Hook. & Thomson.

Guatteria acutiflora Mart. in Mart., Fl. bras. 13(1): 29. 1841, non Wall.
HT: Wied zum Neuwied, M.A.P. s.n. [1816] (BR).

Guatteria acutipetala R.E. Fr., Acta Horti Berg. 12(3): 324. t. 13. 1939.
HT: Ule, E. 3962 (B).

Guatteria acutissima R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 712. 1938.
HT: Klug, G. 1268 (F); IT: NY, US.

[Guatteria aeruginosa Standl., Trop. Woods 16: 11. 1928, nom. nud.]
≡ **Guatteria aeruginosa** Standl.

Guatteria aeruginosa Standl., Publ. Field Columbian Mus. Bot. Ser. 4(8): 206. 1929.
HT: Cooper, G.P. 526 (F); IT: BM, K, US.

Guatteria alata Maas & van Setten, Proc. Kon. Ned. Akad. Wetensch. C. 91(3): 250. figs. 8, 9. 1988.
HT: Alverson, W.S. & al. 1955 (WIS).

Guatteria allenii R.E. Fr., Ark. Bot. n.s. 1(6): 336. 1950.
HT: Allen, P.H. 1900 (S); IT: EAP, F, MO, US.

Guatteria alta R.E. Fr., Ark. Bot. n.s. 1(6): 336. pl. 3. 1950.
HT: Cuatrecasas, J. 14898 (S); IT: COL (2 sheets), F (2 sheets), S, US.

Guatteria alticola Scharf & Maas, Blumea 50: 565. f. 1. 2005.
HT: Clarke & al. 9247 (U); IT: BRG

Guatteria alutacea Diels, Verh. Bot. Vereins Prov. Brandenburg 47: 126. 1905.
HT: Ule, E. 6427 (B); IT: F (fragment), MG, K, L.

Guatteria alutacea Diels var. angustifolia R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 710. 1938.
HT: Spruce, R. 4270 A (B); IT: BM, E, K.
≡ **Guatteria alutacea** Diels f. **angustifolia** (R.E. Fr.) R.E. Fr.

Guatteria alutacea Diels f. **angustifolia** (R.E. Fr.) R.E. Fr., Acta Horti Berg. 12(3): 362. 1939.
HT: Spruce, R. 4270 A (B); IT: BM, E, K.
≡ Guatteria alutacea Diels var. angustifolia R.E. Fr.

Guatteria alutacea Diels var. **steinbachii** R.E. Fr., Acta Horti Berg. 12(3): 362. 1939.
HT: Steinbach, J. 6486 (S); IT: BM, E, F, K, PH.

Guatteria amazonica R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 720. 1938.
HT: Kuhlmann, J.G. s.n. = RB24260 (S); IT: RB 24260.

Guatteria amplifolia Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 35. 1862.
HT: Fendler, A. 3 (K).

Guatteria anomala R.E. Fr., Acta Horti Berg. 12(3): 524. t. 1af. 1939.
HT: von Türckheim, H. 7816 (B); IT: K, US (2 sheets).

Guatteria anthracina Scharf & Maas, Blumea 51: 117. f. 1. 2006.
HT: Lindeman, Stoffers & al. 429 (U); IT: BBS, C, F, NY, S.

Guatteria apodocarpa Mart. in Mart., Fl. bras. 13(1): 30. 1841.
HT: von Martius, C.F.P. s.n. (M).
= **Rollinia parviflora** A. St.Hil.

Guatteria asplundiana R.E. Fr., Ark. Bot. n.s. 4(2): 24. 1959.
HT: Asplund, E. 19673 (S); IT: K, P, S, US.

Guatteria asterantha R.E. Fr., Acta Horti Berg. 12(3): 323. t. 12. 1939.
HT: Mexía, Y. 5485 (S); IT: BM, F, K, U, US.

Guatteria atabapensis Aristeg. ex D.M. Johnson & N.A. Murray, Ann. Missouri Bot. Gard. 77: 599. 1990.
HT: Wurdack, J.J. & Adderley, L.S. 42759 (NY); IT: F, RB.

Guatteria atra Sandwith, Bull. Misc. Inform. 1930: 468. 1930.
HT: Sandwith, N.Y. 406 (K); IT: B, FDG, K (2 sheets), NY, P, RB, U, US.

Guatteria augusti Diels, Notizbl. Bot. Gart. BerlinDahlem 9: 51. 1924.
HT: Weberbauer, A. 7062 (B, 3 sheets); IT: F, S, US.

Guatteria australis A. St.Hil., Fl. Bras. merid. 1: 37. 1825.
HT: de SaintHilaire, A.F.C.P. s.n. (P); IT: P.

Guatteria australis A. St.Hil. var. glabrata Mart. in Mart., Fl. bras. 13(1): 26. 1841.
HT: de SaintHilaire, A.F.C.P. s.n. (P); IT: P.
≡ **Guatteria australis** A. St.Hil.

Guatteria australis A. St.Hil. var. pubens Mart. in Mart., Fl. bras. 13(1): 26. 1841.
HT: von Martius, C.F.P. s.n. [1817] (M).
≡ **Guatteria pubens** (Mart.) R.E. Fr.

Guatteria axilliflora (DC.) R.E. Fr., Acta Horti Berg. 12(3): 427. f. 15a. 1939.
HT: Anonymous collector s.n., French Guiana (G).
≡ Annona axilliflora DC.

Guatteria ayangannae Scharf & Maas, Blumea 50: 565. f. 2. 2005.
HT: Clarke, D. & al. 9819 (U, 2 sheets); IT: BRG, NY (4 sheets).

Guatteria bahiensis R.E. Fr., Acta Horti Berg. 12(3): 408. f. 10a. 1939.
HT: Blanchet, J. s.n. (B).

Guatteria bernardii R.E. Fr., Mem. New York Bot. Gard. 10(2): 23. 1960.
HT: Bernardi, A.L. 6534 (NY); IT: K, S.
= **Guatteria schomburgkiana** Mart.

Guatteria berteriana Spreng., Syst. veg. 2: 635. 1825.
T: Bertero s.n. (TO).
= **Drypetes alba** Poit. (fide Urb., Symb. antill. 4: 340. 1905) {Euphorbiaceae}.

Guatteria bibracteata (Hook.) Hemsl., Diagn. plant. nov. mexic. 1: 1. 1878.
HT: Galeotti 7083 (G).
≡ Annona bibracteata Hook. (= **Desmopsis trunciflora** (Schltdl. & Cham.) G. E. Schatz).

Guatteria blainii (Griseb.) Urb., Symb. antill. 4: 239. 1905.
ST: Wright, C. 1103 (B, G, GOET, K (3 sheets), P).
≡ Asimina blainii Griseb.
≡ Cananga blainii (Griseb.) Britton
≡ Uvaria blainii (Griseb.) M. Gómez
= Uvaria viridiflora Sessé & Moç.

Guatteria blanchetiana R.E. Fr., Acta Horti Berg. 12(3): 331. t. 14. 1939.
HT: Blanchet, J. 2114 (G); IT: BM, F, P.

Guatteria blepharophylla Mart. in Mart., Fl. bras. 13(1): 38. 1841.
ST: von Martius, C.F.P. s.n. (M); Poeppig, E.F. 3110 (B, GOET, P, W).
≡ **Guatteriopsis blepharophylla** (Mart.) R.E. Fr.

Guatteria boliviana H. Winkl., Repert. Spec. Nov. Regni Veg. 7: 242. 1909.
LT: Buchtien, O. 52 (B); IT: E, F, L, NY.

Guatteria boyacana J. F. Macbr., Contr. Gray Herb. 56: 50. 1918.
HT: Whitford & Pinzon 13 (GH); IT: US.
≡ **Pseudomalmea boyacana** (J.F. Macbr.) Chatrou

Guatteria brachypoda R.E. Fr., Kew Bull. 1948: 231. 1948.
HT: Fanshawe, D.B. 738 = Forest Dep. Brit. Guiana 3474 (K, 3 sheets); IT: FDG, NY, S, U.

Guatteria brevicuspis R.E. Fr., Acta Horti Berg. 12(3): 491. f. 28ef. 1939.
HT: Krukoff, B.A. 5589 (S); IT: BM, F (2 sheets), K, MO, NY, RB, U, US.

Guatteria brevipedicellata R.E. Fr., Acta Horti Berg. 12(3): 359. 1939.
HT: Lawrance 771 (S); IT: E, F (2 sheets), G, K (2 sheets), US.

Guatteria brevipes DC. in Dunal, Monogr. Anonac. 126. 1817.
ST: Martin s.n. (BM, G, K, S).
≡ **Cremastosperma brevipes** (DC.) R.E. Fr.

[Guatteria brevipes auct. non DC.: Sagot, Ann. Sci. Nat. Bot. sér. 6. 11: 139. 1881.]
= **Guatteria scandens** Ducke

Guatteria buchtienii R.E. Fr., Acta Horti Berg. 12(3): 388. 1939.
HT: Buchtien, O. 699 (S); IT: US.
= **Guatteria lasiocalyx** R.E. Fr.

Guatteria burchellii R.E. Fr., Acta Horti Berg. 12(3): 398. 1939.
HT: Burchell 2698 (K); IT: P.

Guatteria calimensis R.E. Fr., Ark. Bot. n.s. 1(6): 332. 1950.
HT: Cuatrecasas, J. 16566 (S); IT: COL (3 sheets), F (3 sheets), L, US.

Guatteria calliantha R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 715. 1938.
HT: Tessmann, G. 5164 (B); IT: NY, S.

Guatteria calophylla R.E. Fr., Acta Horti Berg. 12(3): 507. f. 32df. 1939.
HT: Krukoff, B.A. 1534 (S); IT: BM, F, K, MO, NY, P, U, US.

Guatteria calva R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. ser. 3. 24(10): 9. 1948.
HT: Williams, Ll. 14752 (US); IT: F, NY, RB.
= **Guatteria maypurensis** Kunth

Guatteria campestris R.E. Fr., Acta Horti Berg. 12(3): 402. 1939.
HT: Glaziou, A.F.M. 14466 (B); IT: C, K (2 sheets).

Guatteria candolleana Schltdl., Linnaea 9: 325. 1835.
LT: Sellow, F. 5442 p.p. (B), IT: K (2 sheets).
≡ Cananga candolleana (Schltdl.) Warm.
= Guatteria hilariana Schltdl. var. pallescens R.E. Fr.

Guatteria caniflora Mart. in Mart. [var. **caniflora**], Fl. bras. 13(1): 37. 1841.
HT: von Martius, C.F.P. s.n. (M).

Guatteria caniflora Mart. var. **angustifolia** Mart. in Mart., Fl. bras. 13(1): 37. 1841.
HT: von Martius, C.F.P. s.n. (M).

Guatteria caniflora Mart. var. **latifolia** Mart. in Mart., Fl. bras. 13(1): 37. 1841.
HT: von Martius, C.F.P. s.n. [1819] (M).

Guatteria cardoniana R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. ser. 3. 24(10): 9. 1948.
HT: Cardona, F. 1196 (US).

Guatteria cargadero Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 34. 1862.
HT: Triana, J.J. s.n. (P); IT: BM, COL, K, NY, P.

Guatteria caribaea Urb., Symb. antill. 4: 240. 1905.
LT: Sintenis, P. 1535 (B); IT: BM, BP, JE, K, L, M, NY, P, PR, S, US, WU.
≡ Cananga caribaea (Urb.) Britton

Guatteria cauliflora Mart. in Mart., p.p., Fl. bras. 13(1): 35. 1841.
LT: Blanchet, J. s.n. (M).
≡ **Guatteria bahiensis** R.E. Fr.

Guatteria cestrifolia Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 32. 1862.
HT: Triana, J.J. s.n. (P); IT: BM, F (fragment), K, P.

Guatteria chasmantha R.E. Fr., Acta Horti Berg. 12(3): 513. f. 34a. 1939.
HT: Lawrance, A.E. 422 (S); IT: F, G, K, MO, NY, U.

Guatteria chiriquiensis R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. ser. 3. 24(10): 11. 1948.
HT: Pittier, H.F. 5748 (US, 4 sheets).

Guatteria chlorantha Diels, Notizbl. Bot. Gart. BerlinDahlem 9: 139. 1924.
HT: Tessmann, G. 3423 (B); IT: F, NY, S, US (fragment).

Guatteria chocoensis R.E. Fr., Ark. Bot. n.s. 1(6): 333. 1950.
HT: Cuatrecasas, J. 16592 (S, 2 sheets); IT: COL (2 sheets), F, US.

[Guatteria choroniensis Tamayo, Bol. Soc. Venez. Ci. Nat. 7(49): 210. 1942, nom. nud.]

Guatteria chrysopetala (Steud.) Miq., Linnaea 22: 466. 1849.
ST: Hostmann, F.W.A. & Kappler, A. 1295 (ed. Hohen.) (B, BM, G, JE, K, LE, MO, NY, P, PR, OXF, S, U, UPS, W (4 sheets)).
≡ Anona chrysopetala Steud. (= **Guatteria punctata** (Aubl.) R.A. Howard).

Guatteria chrysopetala (Steud.) Miq. var. major R.E. Fr., Acta Horti Berg. 12(3): 435. f. 16ab. 1939.
HT: Ducke, A. RB19612 (S).
= **Guatteria punctata** (Aubl.) R.A. Howard

Guatteria chrysopetala (Steud.) Miq. var. tenuipes R.E. Fr., Acta Horti Berg. 12(3): 435. 1939.
ST: Anonymous collector 239, 249, French Guiana (UPS).
= **Guatteria punctata** (Aubl.) R.A. Howard

Guatteria chrysophylla Maas & van Setten, Proc. Kon. Ned. Akad. Wetensch. C. 91(3): 252. f. 10. l988.
HT: Davis, E.W. & Yost, J. 1011 (NY); IT: F, U.

[Guatteria cinnamomea Wall., Cat. n. 6444. 1832, nom. nud.] [Paleotropics]
T:
≡ **Polyalthia cinnamomea** J.D. Hook. & Thomson.

Guatteria cinnamomea J.D. Hook. & Thomson, Fl. Ind. 1: 138. 1855. [Paleotropics]
T:
≡ **Polyalthia cinnamomea** J.D. Hook. & Thomson.

Guatteria cinnamomea D.R. Simpson, Phytologia 30: 305. 1975, non Wall., nom. illeg.
HT: Jenssen S., E. 133 (F); IT: F (2 sheets), NY, US.

Guatteria citriodora Ducke, Arch. Jard. Bot. Rio de Janeiro 5: 104. t. 2, f. 3ac. 1930.
ST: Ducke, A. RB19609 (F, K, NY, P, S, RB, U, US).

Guatteria clavigera R.E. Fr., Acta Horti Berg. 12(3): 334. f. 5gh. 1939.
HT: Koscinsky, M. 214 (S).

Guatteria clusiifolia D.M. Johnson & N.A. Murray, Ann. Missouri Bot. Gard. 77: 599. 1990.
HT: Tillett, S.S. & al. 45009 (NY); IT: K, MO.
Guatteria coeloneura Diels, Bot. Jahrb. Syst. 37: 408. 1906.
HT: Weberbauer, A. 3548 (B); IT: F (fragment), S (fragment).

Guatteria collina R.E. Fr., Acta Horti Berg. 12(3): 381. 1939.
HT: Goudot, J. s.n. (K); IT: P.

Guatteria columbiana R.E. Fr., Ark. Bot. n.s. 1(6): 335. pl. 2. 1950.
HT: Cuatrecasas, J. 21274 (S); IT: COL (2 sheets), F, S, US (2 sheets).

Guatteria conspicua R.E. Fr., Ark. Bot. n.s. 1(11): 445. f. 1fi. 1950.
HT: Fanshawe, D.B. 2743 = Forest Dep. Brit. Guiana 5542 (K, 3 sheets); IT: FDG, M, NY, S (4 sheets), U.

Guatteria coriacea R.E. Fr., Acta Horti Berg. 12(3): 526. f. 38c. 1939.
HT: Purdie, W. s.n. (K).

Guatteria costaricencis R.E. Fr. [var. **costaricensis**], Acta Horti Berg 12(3): 514. f. 34b. 1939.
HT: Oersted, A.S. 146 (C); IT: S (fragment), US.

Guatteria costaricencis R.E. Fr. var. **endresii** R.E. Fr., Acta Horti Berg. 12(3): 515. 1939.
HT: Endres, A.R. 176 (K); IT: BM.

Guatteria costaricensis R.E. Fr. subsp. panamensis R.E. Fr., Acta Horti Berg. 12(3): 515. 1939.
HT: Cooper, G.P. 382 (F); IT: US.
≡ **Guatteria panamensis** (R.E. Fr.) R.E. Fr.

Guatteria crassipes R.E. Fr., Acta Horti Berg. 12(3): 518. f. 34c. 1939.
HT: Pittier, H.F. 902 (US).

Guatteria cuatrecasasii D. Sánchez, Proc. Kon. Ned. Akad. Wetensch. C. 91(3): 253. f. 12. 1988.
HT: Sánchez, D. & al. 907 (MEDEL); IT: U.

Guatteria cubensis Bisse, Ciencias (México), Ser. 10, Botánica 2: 3. 1975.
HT: Bisse, J. & Areces, A. 16920 (HAJB); IT: HAJB, JE.

Guatteria curvinervia R.E. Fr., Acta Horti Berg. 12(3): 317. t. 11. 1939.
HT: Frazão, A. 8667 (S).

Guatteria curvipetala R.E. Fr., Acta Horti Berg. 12(3): 526. f. 36ab. 1939.
HT: Krukoff, B.A., B.A. 6600 (S); IT: BM, F, G, K, MO, NY, RB, U, US.

Guatteria cuspidata Rusby, Mem. New York Bot. Gard. 7: 245. 1927.
HT: Rusby, H.H. 1706 (NY).
= **Sorocea sprucei** (Baill.) J.F. Macbr. subsp. **sprucei** {Moraceae}.

Guatteria cylindrocarpa R.E. Fr., Ark. Bot. n.s. 3(18): 601. t. 2. 1957.
HT: Schultes, R.E. & López 8949 (US).

Guatteria decandra Ruiz & Pav. ex G. Don, Gen. hist. 1: 100. 1831.
T: Ruiz & Pavón s.n. (MA?).
= Uvaria decandra Ruiz & Pav. ex G. Don, nom. nud.

Guatteria decurrens R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 720. 1938.
HT: Killip, E.P. & Smith, A.C. 29585 (US); IT: F, NY.

Guatteria densicoma Mart. in Mart., Fl. bras. 13(1): 32. 1841.
HT: von Martius, C.F.P. 711 (M); IT: F (fragment), HAL, NY, P.

Guatteria denudata R.E. Fr., Ark. Bot. n.s. 3(18): 601. 1957.
HT: Schultes, R.E. & Cabrera, I. 17374 (S); IT: NY, US.

Guatteria depressa (Baill.) Saff. ex Standl., Contr. U. S. Natl. Herb. 23: 278. 1922.
HT: Liebmann, F.M. 20 (C).
≡ Annona depressa Baill. (≡ **Mosannona depressa** (Baill.) Chatrou subsp. **depressa**).

Guatteria dielsiana R.E. Fr., illegitimate substitute name for G. ucayaliana Diels, Field Mus. Nat. Hist. Bot. Ser. 13(2): 719. 1938.
HT: Tessmann, G. 3212 (B); IT: S.
≡ **Guatteria ucayaliana** Diels

Guatteria dimorphopetala R.E. Fr., Acta Horti Berg. 12(3): 333. f. 5c. 1939.
HT: Sellow, F. 175 (B).

Guatteria diospyroides Baill., Adansonia 8: 269. 1868.
LT: Liebmann, F.M. 12 (C); IT: K, P.
= Guatteria diospyroides · Baill. subsp. hondurensis R. E. Fr.
= Guatteria platypetala · R.E. Fr.

Guatteria diospyroides Baill. subsp. hondurensis R.E. Fr., Acta Horti Berg. 12(3): 378. f. 12b. 1939.
HT: Chickering, J.W. 189 (S); IT: F.
= **Guatteria diospyroides** Baill.

Guatteria discolor R.E. Fr., Acta Horti Berg. 12(3): 509. f. 33a. 1939.
HT: Krukoff, B.A. 7047 (S); IT: BM, F (2 sheets), K, MO, NY, U, US (2 sheets).

Guatteria dolichophylla R.E. Fr., Acta Horti Berg. 12(3): 414. 1939.
HT: Poeppig, E.F. 2693 (BR); IT: F (fragment), HAL, P.
≡ Guatteria inundata Mart. var. longifolia Poepp. ex Mart.

Guatteria dolichopoda Donn. Smith, Bot. Gaz. 23: 2. 1897.
LT: Donnell Smith, J. 6429 (US); IT: C, K (2 sheets), MO, US.

Guatteria dolichopoda Donn. Smith var. **microsperma** R.E. Fr., Acta Horti Berg. 12(3): 358. f. 8a. 1939.
HT: Tonduz, A. 9166 (S); IT: BM, K (2 sheets), M, P, S, US (7 sheets).

[Guatteria dolichopoda auct. non Donn. Smith: Pittier, Prim. fl. costaric. 2(1): 11. 1898.]
= **Guatteria tonduzii** Diels var. **leptopus** R.E. Fr.

Guatteria duckeana R.E. Fr., Acta Horti Berg. 12(3): 468. f. 22fg. 1939.
HT: Ducke, A. s.n. = RB29019 (S); IT: RB.
Guatteria duckeana R.E. Fr. var. subcordata R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. ser. 3. 24(10): 10. pl. 4a. 1948.
HT: Williams, Ll. 15777 (US, 2 sheets); IT: F, NY.

Guatteria dumetorum R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. ser. 3. 24(10): 12. pl. 5. 1948.
HT: Pittier, H.F. 3915 (US, 2 sheets); IT: F.

Guatteria dura R.E. Fr., Acta Horti Berg. 12(3): 499. 1939.
HT: Spruce, R. 3354 (K); IT: BM, K, P.

Guatteria dusenii R.E. Fr., Acta Horti Berg. 12(3): 313. t. 7. 1939.
HT: Dusén, P.K.H. 13752 (S); IT: L, MO.

Guatteria dusenii R.E. Fr. var. **subglabra** R.E. Fr., Acta Horti Berg. 12(3): 313. 1939.
HT: Dusén, P.K.H. 4497 (S).

Guatteria ecuadorensis R.E. Fr., Acta Horti Berg. 12(3): 364. 1939.
HT: Mexía, Y. 7111 (S); IT: F, US.

Guatteria elata R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 712. 1938.
HT: Krukoff, B.A. 8356 (S), IT: BM, F, K, MO, P, U, US.

Guatteria elegans Scharf, Blumea 51: 117. f. 2. 2006.
HT: Feuillet & al. 10256 (NY); IT: U.

Guatteria elegantissima R.E. Fr., Ark. Bot. n.s. 1(6): 338. pl. 4. 1950.
HT: Cuatrecasas, J. 17305 (S); IT: COL (2 sheets), F (2 sheets), L, US.

Guatteria elliptica Blume. [Paleotropics]
T:
= **Polyalthia subcordata** (Blume) Blume.

Guatteria elliptica R.E. Fr., Acta Horti Berg. 12(3): 445. f. 19cd. 1939.
HT: Glaziou, A.F.M. 9605 (C); IT: K, P.

Guatteria elongata Benth., London J. Bot. 2: 359. 1843.
HT: Schomburgk, R.H. I 962 (K); IT: B, BM, E, F, K, L, P, U, US.

Guatteria eriopoda DC. in Dunal, Monogr. Anonac. 130. 1817.
HT: Dombey, J. s.n. (P), IT: F, P.
≡ Uvaria zeylanica Dombey ex Dunal

Guatteria eugeniifolia A. DC. ex R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 714. 1938 ("eugeniaefolia").
HT: Poeppig, E.F. 1859 (G); IT: F, HAL, P (2 sheets).
≡ Guatteria ovalis Mart., not of Ruiz & Pavón

Guatteria excellens R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 721. 1938.
HT: Klug 1273 (F); IT: NY, US.

Guatteria excelsa Poepp. ex Mart. in Mart., Fl. bras. 13(1): 38. 1841.
HT: Poeppig, E.F. 139 (1467) (W); IT: BM, F (fragment), HAL, P.

Guatteria eximia R.E. Fr., Acta Horti Berg. 12(3): 404. 1939.
HT: Pittier, H.F. 13487 (US); IT: F.

Guatteria ferruginea A. St.Hil., Fl. Bras. merid. 1: 38. 1825.
HT: de SaintHilaire, A.F.C.P. s.n. (P); ST : S.
= Guatteria glazioviana R.E. Fr.

[Guatteria ferruginea auct. non. A. St.Hil.: Mart. in Mart. (p.p.), Fl. bras. 13(1): 35. t. 12. 1841.]
≡ **Guatteria burchellii** R.E. Fr.

[Guatteria flava A. St.Hil. in Mart., p.p., Fl. bras. 13(1): 27. 1841.]
Error for: Guatteria lutea A. St.Hil. (= **Guatteria parvifolia** R.E. Fr.).

[Guatteria flava A. St.Hil. in Mart., p.p., Fl. bras. 13(1): 27. 1841.]
Error for: Guatteria lutea A. St.Hil. (≡ **Guatteria lutea** A. St.Hil.).

Guatteria flavovirens R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. ser. 24(10): 10. pl. 4 bd. 1948.
HT: Tamayo, F. 3151 (US); IT: S (fragment).
= **Guatteria schomburgkiana** Mart.

Guatteria flexilis R.E. Fr., Kew Bull. 1952: 255. 1952.
HT: Fanshawe, D.B. 2804 = Forest Dep. Brit. Guiana 5603 (K, 2 sheets); IT: FDG, NY, S (2 sheets), U.

Guatteria foliosa Benth., London J. Bot. 2: 360. 1843.
HT: Schomburgk, R.H. I 995 (K, 3 sheets); IT: BM, E, F (2 sheets), L, NY, P, U, US.

Guatteria fruticosa R.E. Fr., Acta Horti Berg. 12(3): 312. t. 6. 1939.
HT: Löfgren, A. 531 (S).

Guatteria galeottiana Baill., Adansonia 8: 268. 1868.
HT: Liebmann, F.M. 16 (C); IT: F, P.

Guatteria gamosepala R.E. Fr., Acta Horti Berg. 12(3): 528. f. 37ad. 1939.
HT: Krukoff, B.A. 6047 (S); IT: BM, F, K, MO, NY, U, US.

Guatteria gaumeri Greenm., Publ. Field Columbian Mus. Bot. Ser. 2(6): 251. 1907.
ST: Gaumer 189160, 189161, 189976, 189977, 189978 (F).
≡ Malmea gaumeri (Greenm.) Lundell (= **Mosannona depressa** (Baill.) Chatrou subsp. **depressa**).

Guatteria geminiflora R.E. Fr., Acta Horti Berg. 12(3): 421. 1939.
HT: Tessmann, G. 4314 (B); IT: NY.

Guatteria geminiflora R.E. Fr. var. **ochrantha** R.E. Fr., Acta Horti Berg. 12(3): 422. 1939.
HT: Mutis, J. 4486 (US).

Guatteria glaberrima R.E. Fr., Ark. Bot. 33A(9): 3. 1947.
HT: Lugo, M. 237 (S); IT: S, US.

Guatteria glabrescens R.E. Fr., Acta Horti Berg. 12(3): 311. t. 5. 1939.
HT: Kuhlmann, J.G. RB4483 (S); IT: F, RB.

Guatteria glauca Ruiz & Pav., Syst. veg. fl. peruv. chil. 1: 145. 1798.
ST: Ruiz, H. s.n. (B, BR, F, G, HAL (fragment), K, NY, P).

Guatteria glauca (Hassk.) Miq., Fl. Ind. Bat. 1(2): 49. 1858. [Paleotropics]
T:
≡ Uvaria glauca Hassk. (= **Polyalthia glauca** (Hassk.) F. Muell.)

Guatteria glauca Hohen. ex R.E. Fr., Acta Horti Berg, 12(3): 303. 1939, non Ruiz & Pav., nom. illeg.
≡ **Guatteria terminalis** R.E. Fr.

Guatteria glazioviana R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. n.s. 34(5): 19. t. 2, f. 12. 1900.
ST: Glaziou, A.F.M. 6856 (B, C, K, P, S).
= **Guatteria ferruginea** A. St.Hil.

Guatteria gomeziana A. St.Hil., Fl. Bras. merid. 1: 36. 1825.
HT: de SaintHilaire, A.F.C.P. s.n. (P).

Guatteria goudotiana Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 33. 1862.
ST: Goudot, J. 1 (K, P), Triana, J.J. s.n. (P).

Guatteria gracilipes R.E. Fr., Acta Horti Berg. 12(3): 438. f. 17c. 1939.
HT: Krukoff, B.A. 1156 (S); IT: BM, K, NY, P, U.

Guatteria grandiflora Donn. Smith, Bot. Gaz. 14: 25. 1889.
ST: Donnell Smith 1235 (B, K, P, US (2 sheets)).

Guatteria grandiflora Donn. Smith, p.p., Enum. pl. guatem. 6: 2. 1903.
≡ **Guatteria anomala** R.E. Fr.

Guatteria guentheri Diels, Notizbl. Bot. Gart. BerlinDahlem 10: 169. 1927.
HT: Tessmann, G. 4387 (B); IT: F (fragment), NY, S (fragment).

Guatteria guentheriana Diels, Notizbl. Bot. Gart. BerlinDahlem 11: 75. 1931.
HT: Buchtien, O. 1773 (B); IT: F, NY, US.

Guatteria guianensis (Aubl.) R.E. Fr., Acta Horti Berg. 12(3): 505. f. 32ac. 1939.
T: Aublet s.n. (BM).
≡ Aberemoa guianensis Aubl.
≡ Guatteria aberemoa Dunal, nom. illeg.
= Guatteria aberemoa Dunal var. microcarpa DC.

[Guatteria guianensis Klotzsch in M.R. Schomb., Reis. Br.Guiana 3: 1163. 1849, nom. nud.]
= **Guatteria schomburgkiana** Mart. var. **holosericea** R.E. Fr.

Guatteria heteropetala Benth., London J. Bot. 2: 360. 1843.
HT: Schomburgk, R.H. I 950 (K); IT: BM (2 sheets), F, K, L, P, U.
≡ **Heteropetalum brasiliense** Benth.

Guatteria heterotricha R.E. Fr., Acta Horti Berg. 12(3): 392. t. 25. 1939.
HT: Purdie, W. s.n. [1846] (K); IT: K.

Guatteria hilariana Schltdl., Linnaea 9: 324. 1835.
HT: Sellow, F. s.n. (B); IT: HAL.
= Uvaria hirsuta Vell., non Jack.

Guatteria hilariana Schltdl. f. angustifolia Schltdl., Linnaea 9: 324. 1835.
HT: Sellow, F. 5943 (B); IT: HAL.
≡ **Guatteria hilariana** Schltdl. var. **angustifolia** (Schltdl.) Mart.

Guatteria hilariana Schltdl. var. **angustifolia** (Schltdl.) Mart. in Mart., Fl. bras. 13(1): 35. 1841.
HT: Sellow, F. 5943 (B); IT: HAL
≡ Guatteria hilariana Schltdl. f. angustifolia Schltdl.

Guatteria hilariana Schltdl. var. **cuneata** R.E. Fr., Acta Horti Berg. 12(3): 397. 1939.
HT: Burchell, W.J. 3366 (K); IT: K, P.

Guatteria hilariana Schltdl. f. latifolia Schltdl., Linnaea 9: 324. 1835.
HT: Sellow, F. s.n. (B); IT: HAL.
≡ **Guatteria hilariana** Schltdl. var. **latifolia** (Schltdl.) Mart.

Guatteria hilariana Schltdl. var. **latifolia** (Schltdl.) Mart. in Mart., Fl. bras. 13(1): 35. 1841.
HT: Sellow, F. s.n. (B); IT: HAL.
≡ Guatteria hilariana Schltdl. f. latifolia Schltdl.

Guatteria hilariana Schltdl. var. pallescens R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. n.s. 34(5): 15. 1900.
ST: Glaziou, A.F.M. 3855 (B, C).
= **Guatteria candolleana** Schltdl.

Guatteria hilariana Schltdl. var. **verruculosa** R.E. Fr., Acta Horti Berg. 12(3): 397. 1939.
HT: Mosén, H. 3337 (S); IT: P, S.

Guatteria hirsuta Ruiz & Pav., Syst. veg. fl. peruv. chil. 1: 146. 1798.
T: Ruiz, H. s.n. (B, F, HAL).

Guatteria hookeri A. St.Hil. & Tul. ("St.Hil. & Juss.": Index kewensis), Ann. Sci. Nat. Bot. sér. 2. 17: 132. 1842.
HT: Gardner, G. 306 (P); IT: BM (3 sheets), E, F, G, LZ, K (2 sheets), S.

[Guatteria hypoglauca Standl., Trop. Woods 16: 36. 1928, nom. nud.]
= Guatteria hypoglauca Standl. (≡ **Mosannona hypoglauca** (Standl.) Chatrou).

Guatteria hypoglauca Standl., Publ. Field Columbian Mus. Bot. Ser. 4(8): 207. 1929.
HT: Cooper 661 (F); IT: US.
≡ **Mosannona hypoglauca** (Standl.) Chatrou.

Guatteria hyposericea Diels, Notizbl. Bot. Gart. BerlinDahlem 11: 76. 1931.
HT: Williams, Ll. 4129 (F); IT: BM.

Guatteria insculpta R.E. Fr., Acta Horti Berg. 12(3): 504. f. 28ab. 1939.
HT: Spruce, R. 2896 (K, 2 sheets); IT: BM, P.

Guatteria insignis R.E. Fr., Acta Horti Berg. 12(3): 449. 1939.
HT: Krukoff, B.A. 8723 (NY); IT: BM, F, G, K, P, U, US.

Guatteria intermedia Scharf, Blumea 51(3): 545. f. 2. 2006.
HT: Oldeman B.4125 (CAY); IT: NY, P.

Guatteria inuncta R.E. Fr., Acta Horti Berg. 12(3): 378. f. 11a. 1939.
HT: Standley 37132 (US, 2 sheets); IT: F.

Guatteria inuncta R.E. Fr. var. caudata R.E. Fr., Ann. Missouri Bot. Gard. 42: 152. 1955.
HT: von Wedel, H. 2108 (MO); IT: GH.

Guatteria inuncta R.E. Fr. var. minor R.E. Fr., Acta Horti Berg. 12(3): 380. 1939.
HT: Brenes, A.M. 20385 (F); IT: MO.

Guatteria inundata Mart. in Mart., Fl. bras. 13(1): 36. 1841.
HT: von Martius, C.F.P. s.n. [14 Dec. 1819] (M).

[Guatteria inundata auct. non Mart.: Benth., Hooker's J. Bot. Kew Gard. Misc. 2: 360. 1843.]
= **Guatteria obovata** R.E. Fr.

Guatteria inundata Mart. var. longifolia Poepp. ex Mart. in Mart., Fl. bras. 13(1): 36. 1841.
HT: Poeppig, E.F. 2693 (BR).
≡ **Guatteria dolichophylla** R.E. Fr.

Guatteria jamundensis R.E. Fr., Acta Horti Berg. 12(3): 365. f. 8b. 1939.
HT: Ducke, A. MG11780 = RB 35322 (S); IT: RB.

Guatteria jefensis Barringer, Ann. Missouri Bot. Gard. 71: 1186. 1984.
HT: Hammel, B. 6302 (MO).

Guatteria juninensis R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 716. 1938.
HT: Schunke, C. 267 (F, 2 sheets).

Guatteria jurgensenii Hemsl., Diagn. plant. nov. mexic. 1: 1. 1878.
HT: Jürgensen, C. 718 (K); IT: BM (2 sheets).

Guatteria juruensis Diels, Verh. Bot. Vereins Prov. Brandenburg 47: 126. 1905.
HT: Ule, E. 5010 (B); IT: F (fragment), K, L, MG, S (fragment).

Guatteria klotzschiana Mart. in Mart., Fl. bras. 13(1): 32. 1841.
HT: Schott, A.C.V. s.n. (BR); IT: BR, F, US.
≡ Cananga klotzschiana (Mart.) Warm.

Guatteria klugii R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 710. 1938.
HT: Klug, G. 3299 (S); IT: F, K, MO, NY, S, US.

Guatteria knoopiana Pittier, H.F., Bol. Minist. Relac. Exter. (Venezuela) 3: 78. 1927.
HT: Pittier, H.F. 10435 (VEN); IT: G, K, NY, P.
= **Guatteria saffordiana** Pittier

Guatteria krukoffii R.E. Fr., Acta Horti Berg. 12(3): 442. f. 16cd. 1939.
HT: Krukoff, B.A. 1487 (S); IT: BM, F, K, MO, NY, U, US (2 sheets).

Guatteria kuhlmannii R.E. Fr., Acta Horti Berg. 12(3): 498. 1939.
HT: Kuhlmann, J.G. 460 = RB24256 (S); IT: RB.

Guatteria laevigata Mart. in Mart., Fl. bras. 13(1): 32. 1841.
HT: Poeppig, E.F. 2638 (W); IT: BR.
= **Pseudoxandra lucida** R.E. Fr.

Guatteria lanceolata R.E. Fr., Acta Horti Berg. 12(3): 443. f. 18bc. 1939.
HT: Krukoff, B.A. 5950 (S); IT: BM, F, K, MO, NY, U, US (2 sheets).

Guatteria lasiocalyx R.E. Fr., Acta Horti Berg. 12(3): 388. 1939.
HT: Bang, M. 583 (UPS); IT: BM, C, E, F (2 sheets), K, L, MO, S, U, US.
= Guatteria buchtienii R.E. Fr.
= Guatteria pleiocarpa Diels
= Guatteria rhamnoides R.E. Fr.

Guatteria latifolia (Mart.) R.E. Fr., Acta Horti Berg. 12(3): 326. f. 4a. 1939.
HT: Schott, A.C.V. s.n. (BR).
≡ Guatteria nigrescens Mart. var. latifolia Mart.

Guatteria latipetala R.E. Fr., Ark. Bot. n.s. 3(18): 602. t. 3. 1957.
HT: Schultes, R.E. 5512 (US), IT: S (fragment), NY.

Guatteria latisepala R.E. Fr., Acta Horti Berg. 12(3): 368. 1939.
HT: Lehmann, F.C. 27 (S); IT: F, K, S, US.

Guatteria laurifolia Graham, Cat. Bombay Pl. 4. [Paleotropics]
T:
= **Sageraea laurina** Graham.

Guatteria laurifolia (Sw.) Dunal, Monogr. Anonac. 132. t. 32. 1817.
T: Swartz s.n. (S).
≡ Uvaria laurifolia Sw. (≡ **Oxandra laurifolia** (Sw.) A. Rich.).

Guatteria laurina Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 32. 1862.
HT: Goudot, J. s.n. (P); IT: K.

Guatteria lawrancei R.E. Fr., Acta Horti Berg. 12(3): 401. 1939.
HT: Lawrance, A.E. 215 (S), IT: BM, F (2 sheets), K, MO, US (2 sheets).

Guatteria lehmannii R.E. Fr., Acta Horti Berg. 12(3): 395. 1939.
HT: Lehmann, F.C. 4616 (B); IT: F, K.

Guatteria leiocarpa R.E. Fr., Acta Horti Berg. 12(3): 530. f. 36cd. 1939.
HT: Krukoff, B.A. 8995 (S); IT: BM, F, G, K, MO, NY, P, U, US.

Guatteria leiophylla Diels, non (Donn. Smith) Saff. ex Standl, Notizbl. Bot. Gart. BerlinDahlem 11: 77. 1931.
HT: Buchtien, O. 705 (B); IT: S (fragment), US.
≡ **Cremastosperma leiophyllum** R.E. Fr.

Guatteria leiophylla (Donn. Smith) Saff. ex Standl., Publ. Field Columbian Mus. Bot. Ser. 3(3): 268. 1930.
HT: Thieme 5129 (US).
≡ Duguetia leiophylla Donn. Smith (= **Mosannona depressa** (Baill.) Chatrou subsp. **depressa**).

Guatteria leucotricha Scharf & Maas, Blumea 51: 117. f. 3. 2006.
HT: Mori, S. & Boom 15360 (NY); IT: CAY, P, U, US.

Guatteria liesneri D.M. Johnson & N.A. Murray, Ann. Missouri Bot. Gard. 77: 598. 1990.
HT: Nee, M. 30864a (NY); IT: F, U, US.

Guatteria longedecurrens R.E. Fr., Mem. New York Bot. Gard. 10(2): 22. 1960.
HT: Bernardi, A.L. 2255 (NY); IT: K, S.

Guatteria longepetiolata R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. ser. 3. 24(10): 6. pl. 2 ce. 1948.
HT: Cuatrecasas, J. 9185 (US); IT: COL (2 sheets), F, S (fragment).

Guatteria longestipitata R.E. Fr., Acta Horti Berg. 12(3): 438. f. 17ab. 1939.
HT: Ducke, A. RB19613 (S), IT: RB.

Guatteria longicuspis R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. n.s. 34(5): 18. t. 2, f. 35.1900.
HT: Spruce, R. s.n. (B); IT: BM, K, NY, P.
= Duguetia leptocarpa Benth. ex R.E. Fr., nom. nud.

Guatteria longipes Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 32. 1862.
HT: Triana, J.J. s.n. [Sept. 1853] (P); IT: BM, COL, F (fragment), K.

Guatteria lucens Standl., Trop. Woods 42: 22. 1935.
HT: Cooper, G.P. 280 (F); IT: F (2 sheets), G, MO, US.

Guatteria lucida C. Presl, Reliq. Haenk. 2(1): 78. 1835.
HT: Haenke, T. s.n. (PR).

Guatteria lucida Rusby, Mem. New York Bot. Gard. 7: 245. 1927, non C. Presl.
HT: White, O.E. 913 (NY).
≡ Guatteria rusbyi J.F. Macbr. (= **Cremastosperma monospermum** (Rusby) R.E. Fr.)

Guatteria lutea A. St.Hil., Fl. Bras. merid. 1: 37. 1825.
HT: de SaintHilaire, A.F.C.P. s.n. (P).

[Guatteria lutescens Pohl ex Mart. in Mart., Fl. bras. 13(1): 24. 1841, nom. nud.]
≡ **Duguetia pohliana** Mart.

Guatteria macrantha C. Presl, Reliq. Haenk. 2(1): 78. 1831.
HT: Haenke, T. s.n. (PR).

Guatteria macrantha A.DC., Mem. Soc. Phys. Genève 42. 1832. [Paleotropics]
T: Wallich (...)
= **Polyalthia** sp.

Guatteria macrocalyx R.E. Fr., Acta Horti Berg. 12(3): 530. 1939.
HT: Mutis, J. 3705 (US).

Guatteria macrocarpa R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 719. 1938.
HT: Killip, E.P. & Smith, A.C. 28965 (F); IT: NY, US.

Guatteria macropetala R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. ser. 3. 24(10): 7. 1948.
HT: Cuatrecasas, J. 8883 (US); IT: COL, F.

Guatteria macropus Mart. in Mart., Fl. bras. 13(1): 28. t. 8. 1841.
HT: von Martius, C.F.P. 712 (M); IT: BM, F (fragment), HAL, K, L, MO, NY, P, WU.

Guatteria magnifica Ruiz & Pav. ex G. Don, Gen. hist. 1: 100. 1831.
T: Ruiz, H. s.n. [1800] (B).
≡ **Unonopsis magnifolia** R.E. Fr.

Guatteria maguirei R.E. Fr., Mem. New York Bot. Gard. 9(3): 328. 1957.
HT: Maguire, B. & Maguire, C.K. 35231 (S); IT: F, K, NY, US.

Guatteria martiana Schltdl., Linnaea 9: 326. 1835.
HT: Sellow, F. B 1970, C 1483 (B).
≡ **Oxandra martiana** (Schltdl.) R.E. Fr.

Guatteria maypurensis Kunth in Humb., Bonpl. & Kunth, Nov. gen. sp. 5: 64. 1821.
HT: von Humboldt, A. & Bonpland, J. 902 (P); IT: B-Willd., C, HAL.
= Annona lanceolata Willd. ex Steud., nom. nud.
= Annona nitida Willd. ex Steud., nom. nud.
= Guatteria calva R.E. Fr.
= Guatteria maypurensis Kunth var. attenuata R.E. Fr.
= Guatteria maypurensis Kunth var. pulchra R.E. Fr.
= Guatteria velezii R.E. Fr.

Guatteria maypurensis Kunth var. attenuata R.E. Fr., Acta Horti Berg. 12(3): 474. 1939.
HT: Spruce, R. 3077 (K); IT: BM, E, F (fragment), G, HAL, K, NY, P.
= **Guatteria maypurensis** Kunth.

Guatteria maypurensis Kunth var. pulchra R.E. Fr., Acta Horti Berg. 12(3): 474. t. 33. 1939.
HT: Ducke, A. RB29048 (S); IT: MO.
= **Guatteria maypurensis** Kunth.

Guatteria megalophylla Diels, Verh. Bot. Vereins Prov. Brandenburg 47: 127. 1905.
HT: Ule, E. 5630 (B); IT: F, L, MG.
≡ Guatteria megalophylla Diels var. deminuta R.E. Fr.
= Guatteria melosma Diels

Guatteria megalophylla Diels var. deminuta R.E. Fr., Acta Horti Berg. 12(3): 488. f. 26de. 1939.
HT: Krukoff, B.A. 6388 (S); IT: BM, F, K, MO, U, US.
= **Guatteria megalophylla** Diels

Guatteria melinii R.E. Fr., Acta Horti Berg. 12(3): 364. f. 8f. 1939.
HT: Melin, J.B.E. 122 (S).
Guatteria meliodora R.E. Fr., Acta Horti Berg. 12(3): 500. 1939.
HT: Krukoff, B.A. 5050 (S); IT: BM, F, K, MO, NY, U, US.

Guatteria melosma Diels, Notizbl. Bot. Gart. BerlinDahlem 10: 170. 1927.
HT: Tessmann, G. 5039 (B); IT: F, NY.
= **Guatteria megalophylla** Diels

Guatteria metensis R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. ser. 3. 24(10): 6. pl. 2 ab. 1948.
HT: Haught, O.L. 2470 (S); IT: COL, NY, US.

Guatteria mexiae R.E. Fr., Acta Horti Berg. 12(3): 344. 1939.
HT: Mexía, Y. 4249 (S); IT: BM, F (2 sheets), K, U, US.

Guatteria micans R.E. Fr., Acta Horti Berg. 12(3): 451. f. 20b. 1939.
HT: Ducke, A. MG7196 (S); IT: RB.
= **Guatteria scytophylla** Diels

Guatteria microcalyx R.E. Fr., Acta Horti Berg. 12(3): 497. f. 29cd. 1939.
HT: Krukoff, B.A. 1033 (S); IT: BM, K, NY, P, U.

Guatteria microcarpa Ruiz, H. & Pav. ex G. Don, Gen. hist. 1: 100. 1831.
T: Ruiz, H. s.n. (B, HAL).

Guatteria microsperma R.E. Fr., Brittonia 8(4): 236. 1957.
HT: Cowan 38259 (S); IT: NY, RB.

Guatteria minarum R.E. Fr., Acta Horti Berg. 12(3): 346. t. 16. 1939.
HT: Mexía, Y. 5130 (S); IT: BM, F (2 sheets), K, NY, U.

Guatteria minutiflora Scharf & Maas, Blumea 51: 117. f. 4. 2006.
HT: Henkel, T.W. & al. 1156 (U); IT: BRG, US.

Guatteria modesta Diels, Notizbl. Bot. Gart. BerlinDahlem 9: 139. 1924.
HT: Tessmann, G. 3476 (B); IT: F (fragment), NY, S, US (fragment).

Guatteria monticola R.E. Fr., Brittonia 7: 395. 1952.
HT: WilsonBrowne, G. 473 = Forest Dep. Brit. Guiana 5882 (NY, 2 sheets); IT: FDG, K, S.

Guatteria montis-trinitatis Scharf, Blumea 51(3): 548. f. 3. 2006.
HT: De Granville 5947 (U); IT: B, BR, CAY, G, NY, P, US.

Guatteria moralesii (M. Gómez) Urb., Symb. antill. 4: 240. 1905.
ST: C. Wright 1851 (B, BM, G, K, P, S, W).
= Asimina neglecta Griseb.
= Guatteria neglecta (Griseb.) P. Wilson ex León & Alain
≡ Uvaria moralesii M. Gómez
= Uvaria para-neglecta M. Gómez

Guatteria mosenii R.E. Fr., Acta Horti Berg. 12(3): 321. 1939.
HT: Mosén, H. 4002 (S).

[Guatteria multiflora Poepp. ex Baill., Hist. pl. 1: 216. 1868, nom. nud.]
≡ **Bocageopsis multiflora** (Mart.) R.E. Fr.

Guatteria multivenia Diels, Notizbl. Bot. Gart. BerlinDahlem 10: 171. 1927.
HT: Tessmann, G. 5192 (B), IT: F (fragment), NY.

Guatteria myriocarpa R.E. Fr., Acta Horti Berg. 12(3): 458. t. 32. 1939.
HT: Dahlgren, B.E. & Sella, E. 119 (B); IT: F.

Guatteria neglecta R.E. Fr., Acta Horti Berg. 12(3): 308. f. 3a & t. 2. 1939.
HT: Dusén, P.K.H. 6780 (S); IT: F, K, L, MO, NY, P.

Guatteria neglecta (Griseb.) P. Wilson ex León & Alain, Fl. Cuba 2: 178. 1951, non R.E. Fr.
HT: C. Wright 1851 (GOET).
≡ Asimina neglecta Griseb. (= **Guatteria moralesii** (M. Gómez) Urb.).

Guatteria nigrescens Mart. in Mart., Fl. bras. 13(1): 31. 1841.
HT: von Martius, C.F.P. s.n. [1817] (M); IT: B.
≡ Guatteria nigrescens Mart. var. oblongifolia Mart.

Guatteria nigrescens Mart. var. latifolia Mart. in Mart., Fl. bras. 13(1): 31. 1841.
HT: Schott, A.C.V. s.n. (BR).
≡ **Guatteria latifolia** (Mart.) R.E. Fr.

Guatteria nigrescens Mart. var. oblongifolia Mart. in Mart., Fl. bras. 13(1): 31. 1841.
HT: von Martius, C.F.P. s.n. [1817] (M).
≡ **Guatteria nigrescens** Mart.

Guatteria notabilis Mello-Silva & Pirani, Bol. Bot. Univ. São Paulo 10: 44. f. 1-23. 1988.
HT: Mello-Silva, R. & al. CFCR8062 (SPF); IT: F, K, MO, RB, U.

Guatteria novogranatensis R.E. Fr., Acta Horti Berg. 12(3): 496. f. 29ab. 1939.
HT: Lawrance, A.E. 552 (S); IT: BM, COL, F (2 sheets), MO (2 sheets), NY, U.

Guatteria oblanceolata R.E. Fr., Acta Horti Berg. 12(3): 415. 1939.
HT: Krukoff, B.A. 6721 (S); IT: BM, F, K, MO, NY, RB, U, US (2 sheets).

Guatteria obliqua R.E. Fr., Acta Horti Berg. 12(3): 424. f. 14e. 1939.
HT: Kuhlmann, J.G. RB24280 (S); IT: F.

Guatteria oblonga R.E. Fr., Acta Horti Berg. 12(3): 443. f. 19ab. 1939.
HT: Mélinon, E.M. s.n. [1862] (P, 2 sheets) ; IT: B, P, RB.

Guatteria oblongifolia Rusby, Bull. New York Bot. Gard. 4: 320. 1907.
HT: Bang, M. 2232 (NY); IT: F, G, K, MO, US (2 sheets).

Guatteria obovata R.E. Fr., Acta Horti Berg 12(3): 412. f. 14h. 1939.
HT: Schomburgk, R.H. I 922 (K); IT: E, F, G, L, P, U, US.

Guatteria occidentalis R.E. Fr., Acta Horti Berg. 12(3): 430. f. 15b. 1939.
HT: Rose, J.N. & Rose, G. 23429 (US); IT: F, NY.

Guatteria odontopetala Mart. in Mart., Fl. bras. 13(1): 33. t. 11. 1841.
LT: Pohl, J.B.E. 2964 (M); IT: F, G.

Guatteria odorata R.E. Fr., Acta Horti Berg. 12(3): 531. t. 38. 1939.
HT: Ducke, A. s.n. = MG15722 = RB35316 (S); IT: RB.

Guatteria oligocarpa Mart. in Mart., Fl. bras. 13(1): 33. 1841.
HT: von Martius, C.F.P. 714 (M); IT: BM, F, HAL, K, L, MO, NY, P, S, WU.

Guatteria olivacea R.E. Fr., Acta Horti Berg. 12(3): 423. 1939.
HT: Krukoff, B.A. 6853 (S); IT: BM, F, K, MO, NY, U, US.

Guatteria oliviformis Donn. Smith, Bot. Gaz. 23: 1. 1897.
ST: Tonduz, A. 1740 (CR, US); Tonduz 7802 (CR, US).

Guatteria ouregou (Aubl.) Dunal, Monogr. Anonac. 126. 1817.
T: Aublet s.n. (...).
≡ Cananga ouregou Aubl.
≡ Uvaria ouregou (Aubl.) Raeusch.
= Guatteria podocarpa DC.
= Guatteria podocarpa DC. var. oligocarpa DC.
= Guatteria podocarpa DC. var. polycarpa DC.
= Unona crassipetala Dunal
= Unona fuscata DC.
= Unona pachypetala Spreng.
= Uvaria monosperma Lam.

[Guatteria ouregou auct. non Dunal: Griseb., Fl. Brit. W. I. 7. 1859.]
= **Guatteria inuncta** R.E. Fr.

[Guatteria ouregou auct. non Dunal: Mart. in Mart., Fl. bras. 13(1): 36. 1841.]
= **Guatteria pteropus** Benth.

Guatteria ouregou (Aubl.) Dunal var. **latifolia** Sagot, Ann. Sci. Nat. Bot. sér. 6. 11: 138. 1881.
T:

Guatteria ovalifolia R.E. Fr., Acta Horti Berg. 12(3): 428. 1939.
HT: Smith, A.C. 3449 (S); IT: B, F, K, MO, NY, P, U.

Guatteria ovalis Ruiz, H. & Pav., Syst. veg. fl. peruv. chil. 1: 146. 1798.
T: Ruiz, H. & Pavón s.n. (B); IT: F (fragment).
≡ **Ruizodendron ovale** (Ruiz, H. & Pav.) R.E. Fr.

[Guatteria ovalis auct. non Ruiz, H. & Pav.: Mart. in Mart., Fl. bras. 13(1): 38. 1841.]
≡ **Guatteria eugeniifolia** A. DC. ex R.E. Fr.

[Guatteria oxycarpa Poepp. ex Mart. in Mart., Fl. bras. 13(1): 38. 1841, nom. nud., pro syn.]
= Guatteria blepharophylla Mart. (≡ **Guatteriopsis blepharophylla** (Mart.) R.E. Fr.).

Guatteria oxycarpa Miq., Fl. Ind. Bat. 1(2): 49. 1859. [Paleotropics]
T:
= **Polyalthia** sp.

Guatteria pachypetala (Diels) J. F. Macbr., Field Mus. Nat. Hist. Bot. Ser. 4(7): 171. 1929.
HT: Tessmann, G. 4893 (B).
≡ Oxandra pachypetala Diels (≡ **Anaxagorea pachypetala** (Diels) R.E. Fr.).

Guatteria pacifica R.E. Fr., Ark. Bot. n.s. 1(6): 337. 1950.
HT: Cuatrecasas, J. 17150 (S); IT: COL (2 sheets), F (2 sheets), L, S , US (2 sheets).

Guatteria pakaraimae Scharf & Maas, Blumea 50: 568. f. 3. 2005.
HT: Henkel, T.W. & al. 4279 (NY); IT: BRG, U, US.

Guatteria paludosa R.E. Fr., Kew Bull. 1948: 231. 1948.
HT: Fanshawe, D.B. 1045 = Forest Dep. Brit. Guiana 3781 (K, 2 sheets); IT: FDG, NY.

Guatteria panamensis (R.E. Fr.) R.E. Fr., Ark. Bot. n.s. 1(6): 335. 1950.
HT: Cooper, G.P. 382 (F); IT: K.
≡ Guatteria costaricensis R.E. Fr. var. panamensis R.E. Fr.

Guatteria pannosa Scharf & Maas, Blumea 51: 117. f. 5. 2006.
HT: Barrier & Feuillet 2633 (CAY)

Guatteria paraensis R.E. Fr., Acta Horti Berg. 12(3): 464. f. 22ce. 1939.
HT: Ducke, A. RB17866 (S); IT: RB.

Guatteria paranensis R.E. Fr., Acta Horti Berg. 12(3): 314. t. 8. 1939.
HT: Dusén, P.K.H. 6780 (S).

Guatteria partangensis Scharf & Maas, Blumea 50: 569. f. 4. 2005.
HT: Tillett, S.S. & Tillett, C.L. 43975 (K); IT: BRG, MO, NY, S, US.

Guatteria parviflora R.E. Fr., Acta Horti Berg. 12(3): 440. f. 18a. 1939.
HT: Kuhlmann, J.G. RB24263 (S).

Guatteria parvifolia R.E. Fr., Acta Horti Berg. 12(3): 314. t. 9. 1939.
HT: Hoehne, F.C. SP28405 (S); IT: F, K (2 sheets), MO (2 sheets), US.

Guatteria parvifolia R.E. Fr. var. **vestita** R.E. Fr., Acta Horti Berg. 12(3): 315. 1939.
T: Sellow, F. 211 and/or s.n. (B, K, S).

Guatteria pastazae R.E. Fr., Ark. Bot. 33A(9): 5. t. 2. 1947.
HT: Lugo, M. 181 (S); IT: US.

Guatteria pavonii G. Don, Gen. hist. 1: 100. 1831.
T: Ruiz, H. & Pavón s.n. (G, 2 sheets).
≡ **Uvaria longifolia** Ruiz, H. & Pav. ex G. Don

Guatteria peckoltiana R.E. Fr., Acta Horti Berg. 12(3): 457. f. 21c. 1939.
HT: Peckolt, T. 362 (BR).

Guatteria peduncularis (Steud.) Pulle, Receuil Trav. Bot. Néerl. 4: 124. 1907.
ST: Hostmann & Kappler 1116, ed. Hohen. = Hostmann 1116 (BM, K, P, S, U).
≡ Annona peduncularis Steud. (= **Unonopsis guatterioides** (A. DC.) R.E. Fr.).

Guatteria pendula Ruiz, H. & Pav., Syst. verg. fl. peruv. chil. 1: 146. 1798.
T: Pavón s.n. (G).
≡ **Cremastosperma pendulum** (Ruiz, H. & Pav.) R.E. Fr.

Guatteria penduliflora R.E. Fr., Acta Horti Berg. 12(3): 341. t. 15. 1939.
HT: Freire Allemão e Cysneiro s.n. [1860] (G).

Guatteria persicifolia J.D. Hook. & Thomson, Fl. Ind. 1: 140. 1855 ("persicaefolia"). [Paleotropics]
T: Champion s.n. (K).
≡ **Polyalthia persicifolia** (J.D. Hook. & Thomson) Thwaites.

Guatteria persicifolia Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 33. 1862, non J.D. Hook. & Thomson.
HT: Schlim, L.J. 700 (P); IT: BM.

Guatteria peruviana R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 720. 1938.
HT: Killip, E.P. & Smith, A.C. 27522 (US, 2 sheets); IT: NY.

Guatteria petiolata R.E. Fr., Acta Horti Berg. 12(3): 518. f. 34de. 1939.
HT: Lawrance, A.E. 307 (F, 2 sheets), IT: BM, F, K, NY, U.

Guatteria phanerocampta Diels, Notizbl. Bot. Gart. BerlinDahlem 11: 76. 1931.
ST: Williams, Ll. 3436 (F, S, US).

Guatteria pilosula Planch. & Linden ex Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 31. 1862.
HT: Linden, J. 767 (P).

Guatteria pittieri R.E. Fr., Acta Horti Berg. 12(3): 516. 1939.
HT: Pittier, H.F. 531 (US, 2 sheets).

Guatteria platypetala R.E. Fr., Acta Horti Berg. 12(3): 381. f. 11bc & 12c. 1939.
HT: Deam, C.C. 50 (F); IT: US.
= **Guatteria diospyroides** Baill.

Guatteria platyphylla Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 35. 1862.
HT: Triana, J.J. s.n. [Dec. 1853] (P); IT: BM, COL.

Guatteria pleiocarpa Diels, Bot. Jahrb. Syst. 37: 409. 1906.
HT: Weberbauer, A. 4530 (B); IT: F, GH.
= **Guatteria lasiocalyx** R.E. Fr.

Guatteria podocarpa DC. in Dunal, Monogr. Anonac. 127. 1817.
HT: Anonymous collector s.n., French Guiana (P).
= **Guatteria ouregou** (Aubl.) Dunal

Guatteria podocarpa DC. var. oligocarpa DC., Syst. nat. 1: 503. 1818.
HT: Anonymous collector s.n., French Guiana (P).
= **Guatteria ouregou** (Aubl.) Dunal

Guatteria podocarpa DC. var. polycarpa DC., Syst. nat. 1: 503. 1818.
HT: Anonymous collector s.n., French Guiana (P).
= **Guatteria ouregou** (Aubl.) Dunal

Guatteria poeppigiana Mart. in Mart., Fl. bras. 13(1): 36. 1841 ("pöppigiana").
LT: Poeppig, E.F. s.n. (W).

Guatteria pogonopus Mart. in Mart., Fl. bras. 13(1): 34. 1841.
LT: Sellow, F. s.n. (B).

Guatteria pohliana Schltdl., Linnaea 9: 321. 1835.
HT: Sellow, F. 1132(?) (B); IT: K, P.

Guatteria poiteaui Diels, Notizbl. Bot. Gart. BerlinDahlem 11: 74. 1931.
HT: Poiteau s.n. (G); IT: F.
≡ Cremastosperma poiteaui (Diels) R.E. Fr. (= **Cremastosperma brevipes** (DC.) R.E. Fr.).

Guatteria polyantha R.E. Fr., Acta Horti Berg. 12(3): 475. f. 24fg. 1939.
HT: Monteiro da Costa, R. 284 (S); IT: F (2 sheets).

Guatteria polycarpa R.E. Fr., Acta Horti Berg. 12(3): 310. t. 4. 1939.
HT: Dusén, P.K.H. 7414 (S); IT: F, K, L, MO, NY, P.

Guatteria polycarpa R.E. Fr. subsp. **drupacea** R.E. Fr., Acta Horti Berg. 12(3): 311. f. 3c. 1939.
HT: Kuhlmann, J.G. RB19677 (S).

Guatteria ponderosa Rusby, Bull. New York Bot. Gard. 6: 504. 1910.
HT: Williams, R.S. 1479 (NY).
≡ **Porcelia ponderosa** (Rusby) Rusby

Guatteria prinoides Spreng., Syst. veg. 2: 635. 1825.
T: Bertero s.n. (?TO).
= **Drypetes alba** Poit. (fide R.E. Fr., Acta Horti Berg. 12(3): 540. 1939) {Euphorbiaceae}.

Guatteria procera R.E. Fr., Kew Bull. 1948: 230. 1948.
HT: Fanshawe, D.B. 940 = Forest Dep. Brit. Guiana 3676 (K, 2 sheets); IT: FDG, NY, P, S, U.

Guatteria psilopus Mart. in Mart., Fl. bras. 13(1): 27. t. 7, f. 1. 1841.
HT: Luschnath, B. s.n. [1834] (BR).

Guatteria pteropus Benth., Hooker's J. Bot. Kew Gard. Misc. 5: 8. 1853.
HT: Spruce, R. 1680 (K); IT: BM, E, K, NY, P.

Guatteria pteropus Benth. var. **angustior** R.E. Fr., Acta Horti Berg. 12(3): 420. 1939.
HT: Spruce, R. 1342 (K); IT: F (2 sheets), K, P.

Guatteria pteropus Benth. var. **cinerea** R.E. Fr., Acta Horti Berg. 12(3): 420. 1939.
HT: Ducke, A. RB29018 (S); IT: MO, RB.

Guatteria pubens (Mart.) R.E. Fr., Acta Horti Berg. 12(3): 455. f. 21ab. 1939.
HT: von Martius, C.F.P. s.n. [1817] (M).
≡ Guatteria australis A. St.Hil. var. pubens Mart.

[Guatteria pubescens Glaz., Bull. Soc. Bot. France 52. Mém. 3a: 10. 1905, nom. nud.]
= **Annona** sp.

Guatteria pudica N. Zamora & Maas, Bot. Jahrb. Syst. 122: 244. f. 3-5. 2000.
HT: Herrera 4026 (INB); IT: BM, CR, F, MO.

Guatteria punctata (Aubl.) R.A. Howard, J. Arnold Arb. 64: 260. 1983.
T: Aublet s.n. (BM)
= Annona chrysopetala Steud.
≡ Annona punctata Aubl.
= Guatteria chrysopetala (Steud.) Miq.
= Guatteria chrysopetala (Steud.) Miq. var. major R.E. Fr.
= Guatteria chrysopetala (Steud.) Miq. var. tenuipes R.E. Fr.

Guatteria puncticulata R.E. Fr., Acta Horti Berg. 12(3): 511. f. 33bc. 1939.
HT: Krukoff, B.A. 8225 (S), IT: BM, F, K, MO, NY, U, US.

Guatteria quinduensis Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 34. 1862.
HT: Triana, J.J. s.n. (P); IT: BM.

Guatteria raimondii Diels, Notizbl. Bot. Gart. BerlinDahlem 11: 75. 1931.
ST: Raimondi 238 & 1974 (B).
≡ **Mosannona raimondii** (Diels) Chatrou.

Guatteria recurvisepala R.E. Fr., Acta Horti Berg. 12(3): 447. f. 19e. 1939.
HT: Skutch, A.F. 4234 (S); IT: K (2 sheets), MO (2 sheets), S, US.

Guatteria reflexa R.E. Fr., Acta Horti Berg. 12(3): 329. 1939.
HT: Glaziou, A.F.M. 5725 (S); IT: C, F, K, P, RB.

Guatteria reinaldii Erkens & Maas, Blumea 51(2): 206, 210. f. 4. 2006.
HT: Aguilar, R. & al. 4810 (INB).
Guatteria reticulata R.E. Fr., Acta Horti Berg. 12(3): 324. f. 4bd. 1939.
HT: Schwacke, C.A.W. 9155 (B).

Guatteria rhamnoides R.E. Fr., Acta Horti Berg. 12(3): 389. 1939.
HT: Krukoff, B.A. 5707 (S); IT: BM, F (2 sheets), K, MO, NY, RB, U, US.
= **Guatteria lasiocalyx** R.E. Fr.

Guatteria richardii R.E. Fr., Acta Horti Berg. 12(3): 440. 1939.
HT: Richard, L.C. s.n. (P).

Guatteria riedeliana R.E. Fr., Acta Horti Berg. 12(3): 339. f. 6ab. 1939.
HT: Riedel, L. 424 (S); IT: LE.

Guatteria rigida R.E. Fr., Ark. Bot. 5(4): 8. t. 1, f. 12. 1906.
HT: Riedel, L. 438 (S).

Guatteria rigidipes R.E. Fr., Acta Horti Berg. 12(3): 358. t. 21. 1939.
HT: Skutch, A.F. 2553 (S); IT: K, MO, US.

Guatteria riparia R.E. Fr., Acta Horti Berg. 12(3): 410. 1939.
HT: Spruce, R. 3105 (K); IT: BM, C, NY, P.

Guatteria robusta R.E. Fr., Mem. New York Bot. Gard. 9(3): 328. 1957.
HT: Fróes, R.L. 20788 (NY).

Guatteria rostrata Erkens & Maas, Blumea 51(2): 210. t. 2; f. 5. 2006.
HT: Aguilar, R. & al. 3654 (U); IT: CR, INB.

Guatteria rotundata Maas & van Setten, Proc. Kon. Ned. Akad. Wetensch. C. 91(3): 255. f. 11. 1988.
HT: Nee, M. & Tyson, E. 10999 (MO); IT: EAP, H, RB, U.

Guatteria rubrinervis R.E. Fr., Brittonia 7: 395. 1952.
HT: WilsonBrowne, G. 417 = Forest Dep. Brit. Guiana 5816 (NY, 2 sheets); IT: FDG, K, NY.

Guatteria rufa Dunal, Monogr. Anon. 129. t. 29. 1817. [Paleotropics]
T:
≡ **Uvaria rufa** Blume.

Guatteria rufa Triana & Planch., Ann. Sci. Nat. Bot. sér. 4. 17: 35. 1862, non Dunal.
HT: Goudot, J. s.n. (P).
≡ **Guatteria rufotomentosa** R.E. Fr.

Guatteria rufotomentosa R.E. Fr., Acta Horti Berg. 12(3): 392. t. 24. 1939.
HT: Goudot, J. s.n. (P); IT: K.
≡ Guatteria rufa Triana & Planch., non Dunal

Guatteria rugosa R.E. Fr., Acta Horti. Berg. 12(3): 501. 1939.
HT: Krukoff, B.A. 4664 (S); IT: BM, F, G, K, MO, NY, U, US.

Guatteria rupestris Mello-Silva & Pirani, Novon 4(2): 146. 1994.
HT: Pirani, J.R. & al. CFCR12752 (SPF); IT: K, MO, U.

Guatteria rusbyi J.F. Macbr., Publ. Field Columbian Mus. Bot. Ser. 4(7): 171. 1929.
HT: White, O.E. 913 (NY).
≡ Guatteria lucida Rusby, non C. Presl (= **Cremastosperma monospermum** (Rusby) R.E. Fr.).

Guatteria sabuletorum R.E. Fr., Acta Horti Berg. 12(3): 409. t. 27. 1939.
HT: Ducke, A. RB19617 (S); IT: RB.

Guatteria saffordiana Pittier, H.F., Bol. Minist. Relac. Exter. (Venezuela) 3: 77. 1927.
HT: Pittier, H.F. 11855 (VEN); IT: G, K, NY, P, US.
≡ Guatteria knoopiana Pittier

Guatteria sagotiana R.E. Fr., Acta Horti Berg. 12(3): 437. 1939.
HT: Sagot, P.A. 1263 (K); IT: B.

Guatteria sagotiana R.E. Fr. var. **gracilior** R.E. Fr., Acta Horti Berg. 12(3): 437. 1939.
HT: Poiteau, P.A. s.n. (K).
Guatteria salicifolia R.E. Fr., Acta Horti Berg. 12(3): 316. t. 10 & f. 3d. 1939.
HT: Glaziou, A.F.M. 7508 (B); IT: C, K, MG, P.
= **Guatteria glabrescens** R.E. Fr.

Guatteria salicifolia R.E. Fr. var. erosa R.E. Fr., Acta Horti Berg. 12(3): 316. 1939.
HT: Dusén, P.K.H. s.n. [1914] (S); IT: F.

Guatteria sandwithii R.E. Fr., Acta Horti Berg. 12(3): 466. 1939.
HT: Sandwith, N.Y. 1578 (K, 3 sheets); IT: BM, F, NY, P, S, U, US.

Guatteria scalarinervia D.R. Simpson, Phytologia 30: 306. 1975.
HT: Reyna R., N. 40 (F); IT: F (2 sheets), K, NY, P.

Guatteria scandens Ducke, A., Arch. Jard. Bot. Rio de Janeiro 4: 10. 1925.
HT: Ducke, A. s.n. = RB17874 (RB); IT: S.

Guatteria schlechtendaliana Mart. in Mart., Fl. bras. 13(1): 34. 1841.
HT: Von Martius, C.F.P. s.n. (BR).

[Guatteria schlechtendaliana auct. non Mart.: Glaz., Bull. Soc. Bot. France 53, Mém. 3a: 11. 1905.]
≡ Porcelia goyazensis R.E. Fr. (= **Porcelia macrocarpa** (Warm.) R.E. Fr.).

Guatteria schomburgkiana Mart. in Mart., Fl. bras. 13(1): 38. 1841.
HT: Schomburgk, M.R. s.n. (B); ST(?): F.
= Annona hostmannii Steud.
≡ Cananga schomburgkiana (Mart.) Baill.
= Guatteria bernardii R.E. Fr.
= Guatteria flavovirens RE. Fr.
= Guatteria sandwithii R.E. Fr.
= Guatteria schomburgkiana Mart. var. angustifolia Klotzsch ex R. E. Fr.
= Guatteria schomburgkiana Mart. var. latifolia Klotzsch ex R. E. Fr.
= Guatteria sessilis R.E. Fr.
= Guatteria spruceana R.E. Fr.
= Guatteria vestita Klotzsch, nom. nud.
= Guatteria vestita Klotzsch var. angustifolia Klotzsch, nom. nud.
= Guatteria vestita Klotzsch var. latifolia Klotzsch, nom. nud.

Guatteria schomburgkiana Mart. var. b angustifolia Klotzsch ex R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. n.s. 34(5): 17. 1900.
HT: Schomburgk, M.R. 1716 (B).
= **Guatteria schomburgkiana** Mart.

Guatteria schomburgkiana Mart. var. **holosericea** R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 709. 1938.
HT: Klug, G. 2259 (S); IT: BM, F, K, MO, NY, US.

Guatteria schomburgkiana Mart. var. a latifolia Klotzsch ex R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. n.s. 34(5): 17. 1900.
HT: Schomburgk, M.R. 1334 (B).
= **Guatteria schomburgkiana** Mart.

Guatteria schunkevigoi D.R. Simpson, Phytologia 30: 307. 1975.
HT: Schunke V., J. 3551 (F); IT: COL, F, MO, NY, S, US.

Guatteria scytophylla Diels, Verh. Bot. Vereins Prov. Brandenburg 47: 127. 1905.
HT: Ule, E. 5429 (B); IT: K, L, MG.
≡ Guatteria micans R.E. Fr.

Guatteria sellowiana Schltdl., Linnaea 9: 323. 1835.
HT: Sellow, F. B 1967, C 1479 (B); IT: E, K, HAL, P.
≡ Cananga sellowiana (Schltdl.) Warm.
= Cananga sellowiana (Schltdl.) Warm. var. montana Warm.
= Guatteria sellowiana Schltdl. var. montana (Warm.) R.E. Fr.

Guatteria sellowiana Schltdl. var. montana (Warm.) R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. n.s. 34(5): 14. 1900.
HT: Warming, J.E. s.n. (C).
≡ Cananga sellowiana (Schltdl.) Warm. var. montana Warm. (= **Guatteria sellowiana** Schltdl.).

Guatteria sessilicarpa Maas & van Setten, Proc. Kon. Ned. Akad. Wetensch. C. 91(3): 257. f. 13-15. 1988.
HT: Mori, S.A. & Kallunki, J.A. 5037 (MO); IT: U.

Guatteria sessiliflora (Benth.) Saff., Contr. U. S. Natl. Herb. 18: 6. 1914.
HT: Spruce, R. 1668 (K).
≡ Annona sessiliflora Benth. (≡ Guatteriopsis sessiliflora (Benth.) R.E. Fr.) = **Guatteriopsis blepharophylla** (Mart.) R.E. Fr.

Guatteria sessilis R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. n.s. 34(5): 17. t. 2, f. 68. 1900.
HT: Spruce, R. 2661 (C); IT: BM, E, F, G, K, MG, MO, NY, P.
= **Guatteria schomburgkiana** Mart.

Guatteria setosa Rusby, Phytologia 1: 55. 1934.
HT: Tate, G.H.H. 1138 (NY); IT: NY.
= **Guatteria tomentosa** Rusby

Guatteria silvatica R.E. Fr., Acta Horti Berg. 12(3): 330. 1939.
HT: Peckolt, T. 151 (BR).

[Guatteria slateri Standl., Trop. Woods 16: 11. 1928, nom. nud.]
≡ **Guatteria slateri** Standl.

Guatteria slateri Standl., Publ. Field Columbian Mus. Bot. Ser. 4(8): 206. 1929.
HT: Cooper, G.P. & Slater, G.M. 177 (F); IT: NY, US.
= Guatteria slateri Standl., nom. nud.

Guatteria socialis J. F. Macbr., Publ. Field Columbian Mus. Bot. Ser. 4(7): 171. 1929.
HT: Schunke, C. 395 (F).
= **Cremastosperma pedunculatum** (Diels) R.E. Fr.

Guatteria sodiroi Diels in Sodiro, Bot. Jahrb. Syst. 40, Beibl. 91: 42. 1907.
HT: Sodiro, L. 18 (B).

Guatteria sordida R.E. Fr. [var. **sordida**], Acta Horti Berg. 12(3): 532. t. 39. 1939.
ST: Lund, P.W. s.n. and 959 (C).
≡ Guatteria sordida R.E. Fr. var. stenopetala R.E. Fr.

Guatteria sordida R.E. Fr. var. **lancifolia** R.E. Fr., Acta Horti Berg. 12(3): 533. t. 39 p.p. 1939.
HT: Riedel, L. 1689 p.p. (S); IT: K.

Guatteria sordida R.E. Fr. var. **ovalis** R.E. Fr., Acta Horti Berg. 12(3): 533. t. 39 p.p. 1939.
HT: Riedel, L. 1689 p.p. (S); IT: K.

Guatteria sordida R.E. Fr. var. stenopetala R.E. Fr., Acta Horti Berg. 12(3): 533. t. 39 p.p. 1939.
≡ **Guatteria sordida** R.E. Fr. [var. **sordida**].

Guatteria speciosa R.E. Fr., Acta Horti Berg. 12(3): 401. 1939.
HT: Ducke, A. RB29049 (S); IT: K, MO, NY, RB.

Guatteria spectabilis Diels, Notizbl. Bot. Gart. BerlinDahlem 9: 138. 1924.
HT: Tessmann, G. 3235 (B); IT: F (fragment), NY, S, US.

Guatteria sphaerantha R.E. Fr., Ark. Bot. n.s. 1(6): 334. pl. 1. 1950.
HT: Cuatrecasas, J. 17579 (S, 2 sheets); IT: COL (2 sheets), F (2 sheets), US (2 sheets).

Guatteria spruceana R.E. Fr., Acta Horti Berg. 12(3): 469. f 23e. 1939.
HT: Spruce, R. 3698 (K); IT: P.
= **Guatteria schomburgkiana** Mart.

Guatteria stenopetala R.E. Fr., Mem. New York Bot. Gard. 9(3): 329. 1957.
HT: Maguire, B. & al. 36970 (NY); IT: F, S, US.

Guatteria stipitata R.E. Fr., Acta Horti Berg. 12(3): 465. 1939.
HT: Krukoff, B.A. 6907 (S, 2 sheets); IT: BM, F (2 sheets), K, MO, NY, RB, U, US (2 sheets).

Guatteria subsessilis Mart. in Mart., Fl. bras. 13(1): 29. t. 9, f. 1. 1841.
HT: von Martius, C.F.P. s.n. [1819] (M).

Guatteria sylvicola S. Moore, Trans. Linn. Soc. London, Bot. ser. 2. 4: 298. 1895.
HT: Moore, S.L.M. 142 (BM).

Guatteria talamancana N. Zamora & Maas, Bot. Jahrb. Syst. 122: 241. f 1 & 2. 2000.
HT: Aguilar, R. & Morales, F. 4453 (INB); IT: K, MO, U.

Guatteria tenera R.E. Fr., Acta Horti Berg. 12(3): 359. f. 8cd. 1939.
HT: Stork, H.E. 2598 (F); IT: S (fragment).

Guatteria tenuis R.E. Fr., Acta Horti Berg. 12(3): 535. t. 40. 1939.
HT: Mexía, Y. 5482 (S); IT: BM, F (2 sheets), K, MO, U, US.

Guatteria terminalis R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 709. 1938.
HT: Lechler, W. 2648 (UPS); IT: K, LE, P.
≡ Guatteria glauca Hohen. ex R.E. Fr., nom. illeg.

Guatteria tessmannii R.E. Fr., Field Mus. Nat. Hist. Bot. Ser. 13(2): 713. 1938.
HT: Tessmann, G. 4651 (B); IT: NY.

Guatteria tomentosa Rusby, Bull. New York Bot. Gard. 6: 504. 1910.
HT: Williams, R.S. 453 (NY).
= Guatteria trichoclonia Diels

Guatteria tonduzii Diels, Notizbl. Bot. Gart. BerlinDahlem 11: 75. 1931.
HT: Tonduz, A. 17680 (B); IT: BM, F, K, US.

Guatteria tonduzii Diels var. **leptopus** R.E. Fr., Acta Horti Berg. 12(3): 357. 1939.
HT: Pittier, H.F. 10958 (M), IT: C, US.

Guatteria trichoclonia Diels, Notizbl. Bot. Gart. BerlinDahlem 11: 77. 1931.
HT: Buchtien, O. 698 (B); IT: F, S, US.
= Guatteria setosa Rusby
= **Guatteria tomentosa** Rusby

Guatteria trichostemon R.E. Fr., Acta Horti Berg. 12(3): 474. f. 24e. 1939.
HT: Krukoff, B.A. 8862 (S); IT: BM, F, K, MO, NY, P, U, US.

Guatteria ucayaliana Diels, Notizbl. Bot. Gart. BerlinDahlem 9: 138. 1924.
HT: Tessmann, G. 3212 (B); IT: S.
= Guatteria dielsiana R.E. Fr., nom. illeg.

Guatteria ucayalina Huber, Bol. Mus. Paraense Hist. Nat. 4: 560. 1906.
HT: Huber, J.E. 1431 (MG); IT: F (fragment).

Guatteria umbilicata Dunal, Monogr. Anonac. 135. t. 33. 1817.
HT: Forsyth s.n. (G, 2 sheets).
≡ **Unonopsis umbilicata** (Dunal) R.E. Fr.

Guatteria umbonata R.E. Fr., Acta Horti Berg. 12(3): 447. f. 16eg. 1939.
HT: Ducke, A. s.n. = RB19614 (S); IT: RB.

Guatteria umbrosa R.E. Fr., Acta Horti Berg. 12(3): 455. t. 31. 1939.
HT: Riedel, L. s.n. [1823] (S); IT: LE (2 sheets), U.

Guatteria velezii R.E. Fr., Kongl. Svenska Vetensk. Acad. Handl. ser. 3. 24(10): 8. pl. 3. 1948.
HT: Vélez, J. 2488 (S); IT: US.
= **Guatteria maypurensis** Kunth

Guatteria venezuelana R.E. Fr., Acta Horti Berg. 13(3): 110. f. 1ef. 1941.
HT: Delgado, E. 180 (VEN); IT: F (2 sheets), K, S, US.

[Guatteria veneficiorum Mart., Reise Bras. 3: 1237. 1831, nom. nud.]
≡ Guatteria veneficiorum Mart. (≡ **Unonopsis veneficiorum** (Mart.) R.E. Fr.).

Guatteria veneficiorum Mart. in Mart., Fl. bras. 13(1): 34. 1841.
HT: Von Martius, C.F.P. s.n. (M).
≡ **Unonopsis veneficiorum** (Mart.) R.E. Fr.
Guatteria verrucosa R.E. Fr., Acta Horti Berg. 12(3): 519. f. 35a. 1939.
HT: Brenes, A.M. 4058 (F); IT: F.

Guatteria verruculosa R.E. Fr., Ark. Bot. n.s. 3(12): 434. pl. 1. 1956.
HT: Fosberg, F.R. 19126 (S); IT: G, P, US (2 sheets).

[Guatteria vestita Klotzsch in M. R. Schomb., Reis. Br.Guiana 3: 979. 1849, nom. nud.]
= **Guatteria schomburgkiana** Mart.

[Guatteria vestita Klotzsch var. angustifolia Klotzsch in M. R. Schomb., Reis. Br.Guiana 3: 979. 1849, nom. nud.]
= **Guatteria schomburgkiana** Mart.

[Guatteria vestita Klotzsch var. latifolia Klotzsch in M. R. Schomb., Reis. Br.Guiana 3: 979. 1849, nom. nud.]
= **Guatteria schomburgkiana** Mart.

Guatteria villosissima A. St.Hil., Fl. Bras. merid. 1: 38. 1825.
HT: de SaintHilaire, A.F.C.P. 606 (P); IT: P.
≡ Cananga villosissima (A. St.-Hil.) Warm.

Guatteria villosissima A. St.Hil. var. **longepedunculata** R.E. Fr., Acta Horti Berg. 12(3): 351. 1939.
HT: Dusén, P.K.H. 1910 (S).

Guatteria virgata (Sw.) Dunal, Monogr. Anonac. 131. t. 31. 1817, nom. illeg.
T: Swartz s.n. (S).
≡ Uvaria virgata Sw., nom. illeg. (= **Oxandra lanceolata** (Sw.) Baill.).

Guatteria viridiflora Ruiz, H. & Pav. ex G. Don, Gen. hist. 1: 100. 1831.
T: Ruiz, H. & Pavón, J.A. s.n. (...).
= Uvaria viridiflora Ruiz & Pav. ex G. Don, nom. nud.

Guatteria wachenheimii Benoist, Bull. Mus. Hist. Nat. (Paris) 33: 270. 1927.
HT: Wachenheim, G. 201 (P); IT: MO, P, S, US.

Guatteria wesselsboerii Jans.Jac., Proc. Kon. Ned. Akad. Wetensch. C. 73: 336. pl. 1. 1970.
HT: Wessels Boer, J.G. 1302 (U); IT: K, NY.

Guatteria williamsii R.E. Fr., Ark. Bot. n.s. 1(6): 332. 1950.
HT: Williams, Ll. 15559 (S); IT: F, RB, US.

Guatteria wokomungensis Scharf & Maas, Blumea 50: 570. f. 5. 2005.
HT: Boyan, J. 117 = FDG 7941 (NY); IT: FDG.

[Guatteria xalapensis Baill. ex R.E. Fr., Acta Horti Berg. 10(1): 43. 1930, nom. nud.]
= **Mosannona depressa** (Baill.) Chatrou subsp. **depressa**.

Guatteria xanthochlora Diels, Notizbl. Bot. Gart. BerlinDahlem 10: 169. 1927.
HT: Tessmann, G. 4553 (B).
≡ **Mosannona xanthochlora** (Diels) Chatrou.

Guatteria xylopioides R.E. Fr., Acta Horti Berg. 12(3): 459. f. 21g. 1939.
HT: Glaziou, A.F.M. 13401 (B); IT: K, P.

Guatteria zamorae Erkens & Maas, Blumea 51(2): 213. t. 3; f. 6. 2006.
HT: Maas, P.J.M. 9531 (U); IT: INB, K, MO, NY, PMA, SCZ.

Guatteriella campinensis Morawetz & Maas, Pl. Syst. Evol. 148: 20. f. 12. 1984.
HT: Morawetz & D. Coêlho 3124883 (INPA).

Guatteriella tomentosa R.E. Fr., Acta Horti Berg. 12(3): 541. f. 39. 1939.
HT: Ducke, A. RB23916 (S); IT: RB.

Guatteriopsis blepharophylla (Mart.) R.E. Fr., Acta Horti Berg. 12(1): 110. t. 6. 1934.
ST: von Martius, C.F.P. s.n. (M) & Poeppig, E.F. 3110 (B, BM, GOET, P, W).
≡ Guatteria blepharophylla Mart.
= Guatteria oxycarpa Poepp. ex Mart., nom. nud.
= Guatteriopsis sessiliflora (Benth.) R.E. Fr.

Guatteriopsis friesiana W.A. Rodrigues, Acta Amazonica 11(1): 49. f. 1. 1981.
HT: D. Coêlho INPA 3609 (INPA); IT: S.

Guatteriopsis hispida R.E. Fr., Acta Horti Berg. 12(1): 111. t. 7 & 8. 1934.
HT: Ducke, A. RB23903 (S); IT: K, RB, US.

Guatteriopsis kuhlmannii R.E. Fr., Acta Horti Berg. 12(2): 275. t. 8. 1937.
HT: Kuhlmann, J.G. RB24361 (S); IT: RB.

Guatteriopsis ramiflora D. R. Simpson, Phytologia 51: 305. 1982.
HT: Schunke V., J. 3924 (F); IT: COL, F (2 sheets), MO, P, S, U, US.
= **Guatteria** sp.

Guatteriopsis sessiliflora (Benth.) R.E. Fr., Acta Horti Berg. 12(1): 109. 1934.
HT: Spruce, R. 1668 (K); IT: BM, LE, M, NY, W (destr.; photo: MO).
≡ Anona sessiliflora Benth.
= **Guatteriopsis blepharophylla** (Mart.) R.E. Fr.

Heteropetalum brasiliense Benth., J. Proc. Linn. Soc., Bot. 5: 69. 1860.
HT: Schomburgk, R.H. I 950 (K, 2 sheets); IT: BM (2 sheets), F, L, P, U.
≡ Guatteria heteropetala Benth.
= Heteropetalum spruceanum R.E. Fr.
= Heteropetalum spruceanum R.E. Fr. var. longipetalum R.E. Fr.

Heteropetalum spruceanum R.E. Fr., Acta Horti Berg. 10(1): 75. t. 3. 1930.
HT: Spruce, R. 3184 (B); IT: BM, BP, C, E, K, MG, NY, P.
= **Heteropetalum brasiliense** Benth.

Heteropetalum spruceanum R.E. Fr. var. longipetalum R.E. Fr., Mem. New York Bot. Gard. 9(3): 330. 1957.
HT: Maguire, B. & al. 36261 (NY); IT: S.
= **Heteropetalum brasiliense** Benth.

2. INDEX TO PALEOTROPICAL NAMES

Guatteria acuminata Lignur & Bey, Bull. Soc. Linn. Normandie sér.5 5: 168. 1901.
= **?**

Guatteria acutiflora Dunal, Monogr. Anonac. 134. (1817).
= **Polyalthia korinti** (Dunal) Thwaites.

[Guatteria acutiflora Wall., Cat. n. 6438. 1832, nom. nud.]
= **Alphonsea zeylanica** J.D. Hook. & Thomson.

Guatteria bemban Miq., Fl. Ind. Bat. Suppl. 1: 377. 1860.
= **Polyalthia** sp.

Guatteria bifaria A.DC., Mem. Soc. Phys. Genève 41. 1832.
≡ **Polyalthia bifaria** Benth. & J.D. Hook.

Guatteria biglandulosa Blume, Flora Javae (Annonaceae) 102. t. 51. 1828.
≡ **Friesodielsia biglandulosa** (Blume) Steenis.

Guatteria bragma Blume, Bijdr. 20. 1825.
= **? Polyalthia** sp.

Guatteria brevipetala Miq., Fl. Ind. Bat. Suppl. 1: 381. 1861.
= **Trivalvaria macrophylla** (Blume) Miq.

Guatteria canangioides Rchb. f. & Zoll. ex Zoll., Linnaea 29: 322. 1857.
= **Polyalthia rumphii** (Blume ex Hensch.) Merr.

Guatteria cerasoides (Roxb.) Dunal, Monogr. Anonac. 127. 1817
≡ **Polyalthia cerasoides** (Roxb.) Bedd.

[Guatteria cinnamomea Wall., Cat. n. 6444. 1832, nom. nud.]
≡ **Polyalthia cinnamomea** J.D. Hook. & Thomson.

Guatteria cinnamomea J.D. Hook. & Thomson, Fl. Ind. 1: 138. 1855.
≡ **Polyalthia cinnamomea** J.D. Hook. & Thomson.

Guatteria coffeoides Thwaites ex J.D. Hook. & Thomson, Fl. Ind. 1: 141. 1855.
≡ **Polyalthia coffeoides** (Thwaites ex J.D. Hook. & Thomson) Thwaites.

Guatteria cordata Dunal, Monogr. Anonac. 129 t. 30. 1817.
= **Uvaria cordata**costata J.D. Hook.

Guatteria costata J.D. Hook. & Thomson, Fl. Ind. 1: 143. 1855.
≡ **Polyalthia costata** J.D. Hook. & Thomson.

Guatteria cuneiformis Blume, Bijdr. 19. 1825.
≡ **Friesodielsia cuneiformis** (Blume) Steenis.

Guatteria elliptica Blume.
= **Polyalthia subcordata** (Blume) Blume.

Guatteria eriantha Rchb. f. & Zoll., Linnaea 29: 323. 1858.
= **Polyalthia** sp.

Guatteria eupoda Miq., Fl. Ind. Bat. Suppl. 1: 380. 1860.
= **Polyalthia** sp.

Guatteria fragrans Dalzell, Hooker's J. Bot. Kew Gard. Misc. 3: 206. 1851.
≡ **Polyalthia fragrans** (Dalzell) Benth. & J.D. Hook.

Guatteria glauca (Hassk.) Miq., Fl. Ind. Bat. 1(2): 49. 1858.
≡ Uvaria glauca Hassk. (= **Polyalthia glauca** (Hassk.) F. Muell.)

Guatteria globosa A.DC., Mem. Soc. Phys. Genève 43. 1832.
≡ **Miliusa globosa** (A.DC.) Panigr. & S.C. Mishra.

Guatteria hypoleuca Miq., Fl. Ind. Bat. Suppl. 1: 381.
= **Polyalthia glauca** (Hassk.) F. Muell.

Guatteria imbricata Blume, Flora Javae (Annonaceae) 94. t. 46 & 52C. 1828.
= **Goniothalamus costulatus** Miq.

Guatteria jenkensii J.D. Hook. & Thomson, Fl. Ind. 1: 141. 1855.
= **Polyalthia jenkensii** (J.D. Hook. & Thomson) J.D. Hook. & Thomson p.p. & **Polyalthia rumphii** (Blume ex Hensch.) Merr.

Guatteria korinti Dunal, Monogr. Anonac. 133. 1817.
≡ **Polyalthia korinti** (Dunal) Thwaites.

Guatteria lateriflora Blume, Bijdr. 20. 1825.
≡ **Polyalthia lateriflora** (Blume) King.

Guatteria laurifolia Graham, Cat. Bombay Pl. 4.
= **Sagaraea laurina** Graham.

Guatteria littoralis Blume, Flora Javae (Annonaceae) 99. t. 49A. 1828.
≡ **Polyalthia littoralis** (Blume) Boerl.

Guatteria longifolia (Sonn.) Wall., Cat. 6442. 1832.
≡ **Polyalthia longifolia** (Sonn.) Thwaites.

Guatteria macrantha A.DC., Mem. Soc. Phys. Genève 42. 1832.
= **Polyalthia** sp.

Guatteria macrophylla A.DC., Mem. Soc. Phys. Genève 5: 217. 1832.
= **?**

Guatteria macrophylla Blume, Bijdr. 19. 1825.
= **Trivalvaria macrophylla** (Blume) Miq.

Guatteria macropoda Zipp. ex Burck, Nova Guinea 8: 429. 1911.
= **?**

Guatteria malabarica Dunal, Monogr. Anon. 134. 1817.
= **Uvaria zeylanica** Lour.

Guatteria membranacea A.DC., Mem. Soc. Phys. Genève 41. 1832.
≡ **Polyalthia membranacea** (A.DC.) J.D. Hook. & Thomson.

Guatteria micrantha A.DC., Mem. Soc. Phys. Genève 42. 1832.
≡ **Cyathostemma micranthum** (A.DC.) J. Sincl.

Guatteria montana A.DC., Syst. 1: 508. 1818.
= **Uvaria zeylanica** Lour.

Guatteria multinervis Wall., Cat. 6445. 1832, nom. nud.
= **?**

Guatteria nitida A.DC., Mem. Soc. Phys. Genève 41. 1832.
≡ **Enicosanthum nitidum** (A.DC.) Airy-Shaw.

Guatteria oxycarpa Miq., Fl. Ind. Bat. 1(2): 49. 1859.
= **Polyalthia** sp.

Guatteria palembanica Miq., Fl. Ind. Bat. Suppl. 1: 379. 1861.
= **Polyalthia cauliflora** J.D. Hook. & Thomson.

Guatteria pallida Blume, Bijdr. 20. 1825.
= **Marsypopetalum pallidum** (Blume) Backer.

Guatteria pallida J.D. Hook. & Thomson, Fl. Ind. 1: 143. 1855.
≡ **Trivalvaria argentea** (J.D. Hook. & Thomson) J. Sincl.

Guatteria parveana Miq., Fl. Ind. Bat. 1: 48. 1858.
= **Polyalthia rumphii** (Blume ex Hensch.) Merr.

Guatteria persicifolia J.D. Hook. & Thomson, Fl. Ind. 1: 140. 1855 ("persicaefolia").
≡ **Polyalthia persicifolia** (J.D. Hook. & Thomson) Thwaites.

Guatteria pilosa G.Don, Gen. Syst. 1: 100.
= **Uvaria hirsuta** Jack.

Guatteria pisocarpa Blume, Bijdr. 2. 1825.
≡ **Popowia pisocarpa** (Blume) Endl.

Guatteria pondok Miq. Fl. Ned. Ind., Eerste bijv. 1: 380. 1860.
≡ **Polyalthia pondok** (Miq.) Boerl.

Guatteria ramosissima Wall., Cat. 7294 & 8006. 1832-47, nom. nud.
= **Popowia pisocarpa** (Blume) Endl.

Guatteria rufa Dunal, Monogr. Anon. 129. t. 29. 1817.
≡ **Uvaria rufa** Blume.

Guatteria rumphii Blume ex Henschel, Vita Rumphii 153. 1833.
≡ **Polyalthia rumphii** (Blume ex Hensch.) Merr.

Guatteria sempervirens Dunal, Monogr. Anonac. 133. 1817.
= **Polyalthia** sp.

Guatteria sesquipedalis Wall., Pl. As. Rar. 3 t. 266. 1832.
≡ **Goniothalamus sesquipedalis** (Wall.) J.D. Hook. & Thomson.

Guatteria simiarum Hamilton ex J.D. Hook. & Thomson, Fl. Ind. 1: 142. 1855.
≡ **Polyalthia simiarum** Benth. & J.D. Hook.

Guatteria spathulata Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indië 25: 420. (1863)
≡ **Polyalthia spathulata** (Teysm. & Binn.) Boerl.

Guatteria suberosa (Roxb.) Dunal, Monogr. Anonac. 128. 1817.
≡ **Polyalthia suberosa** (Roxb.) Thwaites.

Guatteria sumatrana Miq., Fl. Ind. Bat. Suppl. 1: 380. 1861.
≡ **Polyalthia sumatrana** (Miq.) Kurz.
Guatteria teysmannii Miq., Fl. Ind. Bat. Suppl. 1: 378. 1861.
= **Polyalthia cauliflora** J.D. Hook. & Thomson.

Guatteria toralak Blume, Flora Javae (Annonaceae) 103. t. 53A. 1828.
= **Polyalthia** sp.

Guatteria unoniaefolia A.DC., Mem. Soc. Genève 5: 41. 1832.
= **? Friesodielsia**

Guatteria velutina (Dunal) A.DC., Mem. Soc. Genève 5: 42. 1832.
≡ Uvaria velutina Dunal (≡ **Miliusa velutina** (Dunal) J.D. Hook. & Thomson).

Guatteria villosa G.Don, Gen. Syst. 1 : 100.
= **Miliusa velutina** (Dunal) J.D. Hook & Thomson.

REFERENCES

Bridson, G. D. R. & Smith, E. R. (eds.) 1991. *Botanico-Periodicum-Huntianum/Supplementum*. Hunt Institute for Botanical Documentation, Pittsburgh.

Brummitt, R. K. & Powell, C. E. (eds.). 1992. *Authors of Plant Names*. Royal Botanical Gardens, Kew.

Holmgren, P. K., Holmgren, N. H. & Barnett, L. C. 1990. Index Herbariorum. Part I: The herbaria of the world, ed. 8. *Regnum Vegetabile* 120.

Keßler, P. J. A., Jessup, L. W. and Kruijer, J. D. 1995. Provisional checklist of the Asiatic-Australian species of Annonaceae.

Lawrence, G. H. M., Buchheim, A. F. G., Daniels, G. S., Dolezal, H. (eds.). 1968. *Botanico-Periodicum-Huntianum*. Hunt Botanical Library, Pittsburg, Pa.

Maas, P. J. M., Mennega, E. A. and Westra, L. Y. Th. 1994. Studies in Annonaceae. XXI. Index to species and infraspecific taxa of Neotropical Annonaceae.

Rainer, H. & Chatrou, L. W. 2006. The World Species List of Annonaceae - version 1.0, Published on the internet: http://www.annonaceae.org and http://www.sp2000.org/

Stafleu, F. A. and Cowan, R. S. 1976-1987. *Taxonomic Literature*, 7 vols. Bohn, Scheltema & Holkema, Utrecht; W. Junk, The Hague.

NEDERLANDSE SAMENVATTING

In de Neotropen[1] kan men ongeveer 30% van alle plantensoorten vinden. Hoe al deze soorten daar gekomen zijn is nog steeds onduidelijk. Verplaatsing van soorten uit een ander gebied de Neotropen in, kan een verklaring zijn. Een aantal recente studies suggereren dit ook. Er zijn echter meer onderzoeken nodig om deze hypothese te onderbouwen. *Guatteria*, het grootste plantengeslacht uit de familie van de Zuurzakken (Annonaceae in het latijn), bestaat uit ongeveer 290 soorten, veelal bomen, en kan in de gehele Neotropen worden gevonden. Juist omdat het geslacht zo een breed verspreidingsgebied heeft en de soorten veel voorkomen, kan *Guatteria* als model dienen om het ontstaan van soorten te onderzoeken.

In dit proefschrift wordt onder andere de evolutionaire geschiedenis van *Guatteria* onderzocht (hoofdstuk 4). Drie belangrijke gebeurtenissen in de geschiedenis van dit plantengeslacht zijn hierbij gereconstrueerd: (1) eerst vond een migratie plaats over de oceaan tussen Centraal en Zuid Amerika meer dan 6 miljoen jaar geleden. Dit was dus vóórdat de huidige landbrug van Panama gesloten was (dat gebeurde pas zo'n 3,5 miljoen jaar geleden); (2) na deze migratie vormde zich het merendeel van de huidige *Guatteria* soorten in Zuid Amerika; (3) tot slot waren er verschillende remigraties van Zuid Amerikaanse soorten naar Centraal Amerika. Dit gebeurde ná het sluiten van de landbrug van Panama. Met deze resultaten bevestigd deze studie het eerder gevonden resultaat: verplaatsing van soorten de Neotropen in heeft mogelijk een belangrijke bijdrage geleverd aan de hoge biodiversiteit daar.

Tevens is ook de bestaande indeling van de verschillende *Guatteria* soorten in groepen (zogenaamde "secties") en de relatie van *Guatteria* met drie kleine andere geslachten (*Guatteriopsis, Guatteriella* en *Heteropetalum*) bestudeerd (hoofdstuk 5). De huidige indeling is gebaseerd op morfologie (uiterlijke kenmerken, zoals de vorm van de vrucht of de bloemblaadjes). Hierdoor zijn de meeste soorten moeilijk uit elkaar te houden. Vanwege deze complexiteit zijn de meeste wetenschappers terughoudend geweest om een grote studie aan *Guatteria* te wijden. Hierdoor dateert de laatste grote studie van dit geslacht uit 1939. In dit proefschrift is daarom een andere benadering gekozen. Er worden zogenaamde "stambomen" gemaakt (zie bijvoorbeeld pagina 73), die de evolutionaire relaties tussen de hedendaagse soorten weergeeft. Dit is gedaan door het DNA[2] uit de chloroplasten[3] van ongeveer 40% van alle *Guatteria* soorten te vergelijken. Helaas was dit nog onvoldoende om een goed inzicht te krijgen in álle relaties tussen de soorten. Daarom kan er nog steeds geen compleet nieuwe indeling van *Guatteria* worden opgesteld. Het is echter wel duidelijk geworden dat het grootste deel van de bestaande indeling niet meer voldoet. Ondanks deze problemen, konden er wel enige conclusies worden getrokken over de morfologische evolutie binnen het geslacht. Een morfologische nachtmerrie voor taxonomen[4] in de afgelopen tientalle jaren, blijkt zelfs nu nog gedeeltelijk een mysterie te zijn voor biologen, die met de allermodernste technieken werken.

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[1] de Neotropen is een gebied dat loopt van Mexico tot Zuid Brazilië

[2] het erfelijke materiaal (o.a. de genen), dat in alle levende wezens te vinden is

[3] de onderdelen van het blad, die energie uit zonlicht vastleggen. De chloroplasten zijn groen en geven daarom het blad zijn groene kleur

[4] biologen die zich bezig houden met het indelen van de levende wereld

De Centraal Amerikaanse *Guatteria* soorten zijn over het algemeen makkelijker uit elkaar te houden dan de Zuid Amerikaanse *Guatteria* soorten. Om deze soorten beter te kunnen bestuderen, is veldwerk uitgevoerd in Costa Rica en Panama. Gedurende dit veldwerk werden vijf nieuwe *Guatteria* soorten ontdekt (hoofdstuk 9). Deze vijf soorten zijn bestudeerd, samen met de andere reeds bekende Centraal Amerikaanse soorten. Het resultaat van deze studie is een bewerking voor *Flora Mesoamericana*[1] (hoofdstuk 10). Naast de beschrijvingen van de soorten zijn ook foto's opgenomen, zodat specialisten en niet-specialisten met behulp van dit hoofdstuk de namen van *Guatteria* soorten uit Centraal Amerika kunnen opzoeken. Tot slot is in hoofdstuk 11 een lijst te vinden van inheemse plantennamen. Ieder plant heeft een latijnse wetenschappelijke naam, maar vaak kent de locale bevolking deze naam niet. Om toch aan deze mensen te kunnen vragen waar bepaalde planten zich bevinden, is deze lijst samen gesteld.

Omdat het niet mogelijk was om van alle in dit proefschrift gebruikte soorten zelf materiaal te gaan verzamelen, is er veel gebruik gemaakt van herbariummateriaal (op papier opgeplakte planten). De kleur of de leeftijd van de gedroogde planten kan een voorspellende waarde hebben voor het succes waarmee DNA uit het blad kan worden gehaald. Om te kijken of jongere en/of groenere bladeren beter zijn om te gebruiken, dan oudere en bruinere bladeren, is een apart onderzoek gedaan (hoofdstuk 7). Verassend genoeg blijkt zowel leeftijd als kleur niet altijd een goede voorspeller te zijn voor het succes waarmee DNA uit het blad kan worden gehaald.

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[1] In een Flora staat beschreven hoe afzonderlijke planten uitzien en hoe deze uit elkaar te houden zijn. *Flora Mesoamericana* gaat specifiek over de planten in Centraal America.

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CURRICULUM VITAE (SELECTED ITEMS)

PUBLISHED ARTICLES

Erkens, R. H. J., Maas, P. J. M., Chatrou, L. W., Schatz, G. E. & Zamora, N. 2006. Seven taxonomic discoveries in Annonaceae from southeastern Central America. *Blumea* 51: 199-220.

Pirie, M. D., Chatrou, L. W., Mols, J. B., Erkens, R. H. J. & Oosterhof, J. 2006. 'Andean-centred' genera in the short-branch clade of Annonaceae: Testing biogeographic hypotheses using phylogeny reconstruction and molecular dating. *J. Biogeogr.* 33: 31-46.

Pirie, M. D., Chatrou, L. W., Erkens, R. H. J., Maas, J. W., van der Niet, T., Mols, J. B. & Richardson, J. E. 2005. Phylogeny reconstruction and molecular dating in four Neotropical genera of Annonaceae: the effect of taxon sampling in age estimations. Pp. 149-174 in: Bakker, F. T., Chatrou, L. W., Gravendeel, B. & Pelser, P. B., (Eds.), *Plant species-level systematics: new perspectives on pattern and process*, Regnum Vegetabile 143, A. R. G. Gantner Verlag, Liechtenstein.

Richardson, J. E., Chatrou, L. W., Mols, J. B., Erkens, R. H. J. & Pirie, M. D. 2004. Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae. *Phil. Trans. R. Soc. Lond. B* 359: 1495-1508.

EDITORSHIP

Annonaceae systematics over time, **L. W. Chatrou, H. Rainer, J. E. Richardson & R. H. J. Erkens** (Eds.). A.R.G. Gantner Verlag, Ruggell, Liechenstein (Regnum Vegetabile, in preparation).

POSTER PRESENTATION

Erkens, R. H. J., Chatrou, L. W. , Maas, J. W., Hoenselaar, K., Csiba, L. & Maas, P. J. M. 2005. Evolution of the large and widespread Neotropical genus *Guatteria* (Annonaceae). XVII International Botanical Congress, Vienna.

INTERNATIONAL PRESENTATIONS

2005 Systematics 5 Congress, Cardiff
2005 Annonaceae workshop, Vienna
2003 Systematics 4 Congress, Dublin
2002 Annonaceae workshop, Malaga
2002 Young Systematist Meeting, London
2001 Young Systematist Meeting, London

AWARDS & QUALIFICATIONS

2005 Best Oral Presentation Award, Systematics 5 Congress, Cardiff
2004 Basic Qualification in University teaching, Utrecht University
2003 Young Teacher Talent Award, Utrecht University
2003 Shell Personal Development Award