Extranuptial nectaries in *Carapa* Aubl. (Meliaceae-Cedreloideae)

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ABSTRACT
Ant-plant interactions mediated by special structures provided by plants such as domatia, extrafloral nectaries (EFNs) and food bodies, are very frequent in tropical ecosystems. To understand why ants are frequently encountered on most species of *Carapa* Aubl. (Meliaceae), we investigated the presence of extranuptial nectaries (ENNs) in all 27 species of the genus, spanning its entire distributional range in tropical Africa and America. We report for the first time in the genus the occurrence of extrafloral nectaries (at the base of the petiole, along the rachis of the pinnately compound leaf, on bracts) petaline nectaries (on the outer surface of petals), and pericarpial nectaries (on the surface of fruits), and confirm the presence of nectaries on leaflets in *Carapa*. Petiolar nectaries are the most common, occurring in 85% of the species. Nectaries were mainly active in young developing plant organs. Ants were observed foraging on exudates from these nectaries. The secretions from these glands help to explain the abundance of ants on *Carapa* trees. Although similar nectaries were also found in other members of the subfamily Cedreloideae, their position and frequency provide new characters for the identification of *Carapa* species in the field and the herbarium. As in other myrmecophilous plants, ENNs probably confer adaptive advantages to *Carapa* trees.

KEY WORDS
Carapa,
extrafloral nectaries,
Meliaceae,
myrmecophily,
pericarpial nectaries,
petaline nectaries.

RÉSUMÉ

Nectaires extranuptiaux chez les Carapa *Aubl. (Meliaceae-Cedreloideae).*

Les interactions plantes-fourmis entretenues par des organes spécialisés tels que les domaties, les nectaires extrafloraux (NEF) et les organes nourriciers, sont très fréquentes dans les écosystèmes tropicaux. Pour comprendre pourquoi les fourmis sont fréquemment rencontrées sur la plupart des espèces de *Carapa* Aubl. (Meliaceae), nous avons recherché la présence des nectaires extranuptiaux (NENs) chez les 27 espèces du genre, couvrant toute son aire de distribution en Afrique tropicale et en Amérique. Nous signalons pour la première fois dans le genre *Carapa* la présence des nectaires extrafloraux (à la base du pétiole, le long du rachis de la feuille composée-pennée, sur les bractées), des nectaires pétalaires (à la face extérieure des pétales), des nectaires péricarpiaux (à la surface des fruits), et confirmons la présence des nectaires sur les folioles. Les nectaires pétiolaires sont les plus fréquents, présents dans 85 % des espèces. Les nectaires sont principalement actifs sur les organes jeunes en cours de développement. Les fourmis ont été observées en train de récolter des exsudats de ces nectaires. Les sécrétions de ces glandes permettent d'expliquer l'abondance des fourmis sur les *Carapa*. Bien que des nectaires similaires aient également été observés chez d'autres membres de la sous-famille des Cedreloideae, la variation de leur position et leur fréquence fournissent de nouveaux caractères pour l'identification des espèces de *Carapa* sur le terrain et en herbier. Comme chez d'autres plantes myrmécophiles, les NENs confèrent probablement des avantages adaptatifs aux espèces de *Carapa*.

MOTS CLÉS
Carapa,
Meliaceae,
myrmécophilie,
nectaires extrafloraux,
nectaires péricarpiaux,
nectaires pétalaires.

INTRODUCTION

Mutualistic interactions between plants and ants have developed probably since the mid-Cretaceous and are today very common, ranging from facultative non-specific relationships to obligatory specific and symbiotic associations (Hölldobler & Wilson 1990; Bronstein 1998; Solano & Dejean 2004). Mutualistic ant-plant interactions are mediated by resource rewards provided either indirectly by honeydew-producing insects (Compton & Robertson 1988; Blüthgen *et al.* 2000; Crutsinger & Sanders 2005) or directly by the plants. Plant-produced rewards include domatia (hollow structures), food bodies (Fiala *et al.* 1989; Dutra *et al.* 2006), and extranuptial nectaries (Oliveira 1997; Koptur 2005), which are the focus of this paper.

The term extranuptial nectaries (ENNs) is commonly used in accordance with Delpino's (1874) functional definition to designate plant organs that produce nectar for functions other than direct attraction of pollinators. The location of ENNs varies among taxa. These structures may occur on reproductive structures (petals, flower buds, fruits) or vegetative organs (petiole, rachis, lamina, stipules, and stem). ENNs have been reported in over 4000 species of vascular plants, belonging to 745 genera and 113 families (Zimmermann 1932; Elias 1983; Koptur 1992; Keeler 2008). In Meliaceae, these structures are documented in eight genera and 15 species belonging to both subfamilies Melioideae and Cedreloideae. They may occur on leaflet surfaces, petioles, rachis, petals, sepals or fruits (Zimmermann 1932; Lersten & Rugenstein 1982; Elias 1983 ; Lersten & Pohl 1985; Schupp & Feener 1991; Puri 1999; Blüthgen & Reifenrath 2003; Mody & Linsenmair 2004; Díaz-Castestelazo *et al.* 2004). While field observations reveal the frequent

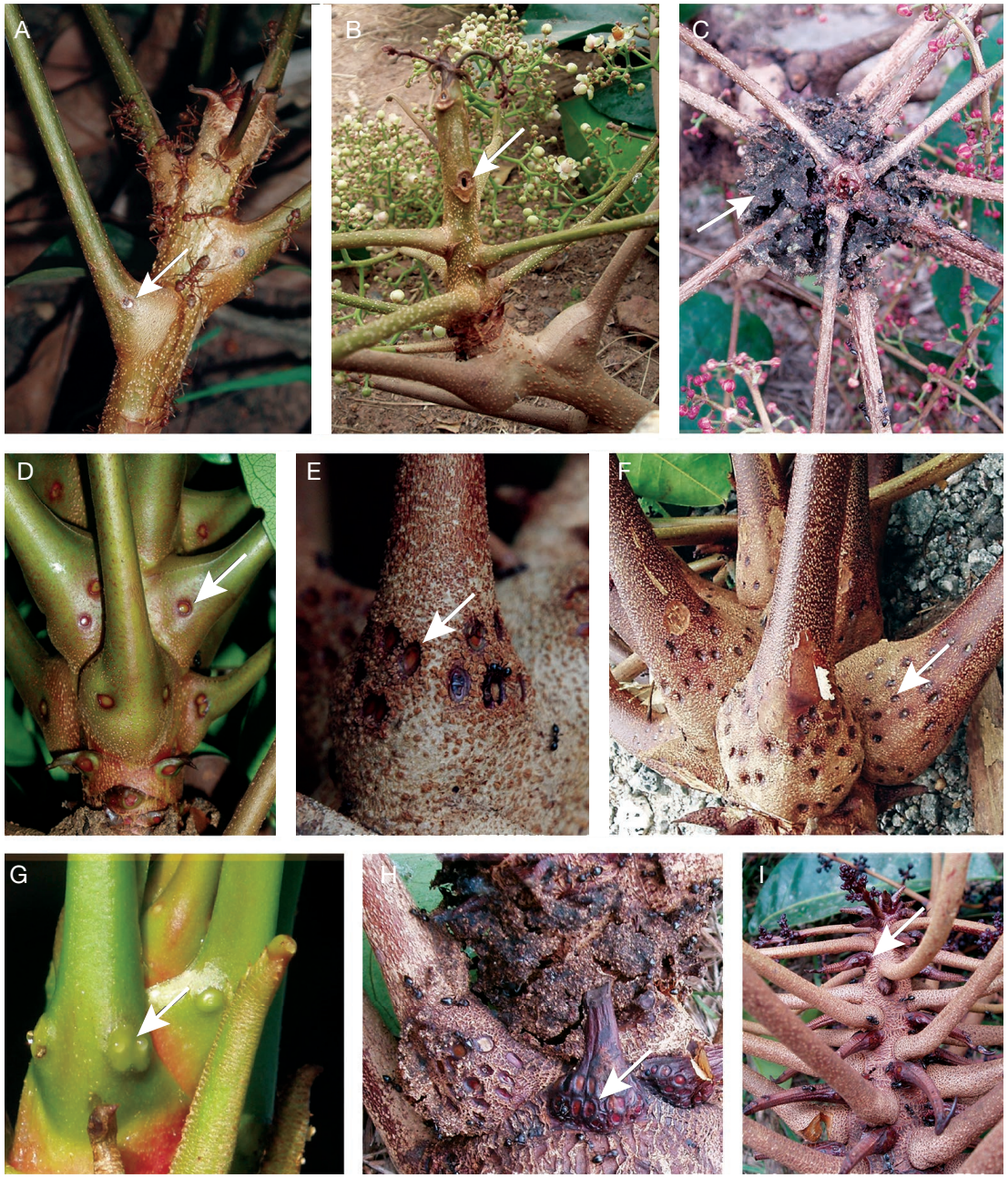

Fig. 1 — Extrafloral nectaries in *Carapa* Aubl.: **A**, ants on a *C. procera* C.DC. twig in Ejura, Ghana; **B**, ant chamber on the inflorescence of *C. procera* in Casamance, Senegal; **C**, ant nest on the inflorescence of *C. parviflora* Harms near Libreville, Gabon; **D**-**G**, petiolar nectaries in *C. microcarpa* A. Chev. in Ghana (**D**), *C. parviflora* in Korup National Park, Cameroon (**E**), *C. macrantha* Harms near Makokou, Gabon (**F**), and *C. guianensis* Aubl. in Waini River, Guyana (**G**); **H**, **I**, petiolar nectaries on inflorescence bracts in *C. parviflora* near Libreville, Gabon (**H**) and *C. macrantha* near Makokou, Gabon (**I**).

occurrence of ants on *Carapa* Aubl. trees (Fig. 1A-C), we are not aware of any attempt to investigate a potential explanation for this prevalence.

In this paper, based on field observations and herbarium studies, we provide evidence of the presence of ENNs on numerous plant parts in *Carapa*. We focus only on the morphology and typology of the nectaries, without any histological or physiological scope, and include all 27 species currently recognized in the genus.

MATERIAL AND METHODS

The investigation was conducted within the framework of a revision of *Carapa*, a genus of Meliaceae that comprises 27 species of small to large trees distributed throughout tropical forests in Africa and America (Kenfack 2008, 2011). The study included field observations on living plants in Africa (Cameroon, Gabon, Ghana, Senegal) and the Americas (Ecuador, Guyana and Panama), and herbarium investigations of specimens from important herbaria holding material from these regions, including BR, F, GH, K, MO, NY, P and US. Our attention was first caught by the abundance of ENNs and ant activity in *Carapa macrantha* Harms (taxonomic authorities are provided in Table 1) during fieldwork in Gabon. Subsequently, observations were extended to the other members of the genus and finally, for comparison, to representatives of the remaining thirteen genera of the subfamily Cedreloideae (Table 1). During fieldwork, direct observations were made on 21 species of *Carapa* (Table 1). For the herbarium studies, a dissecting microscope was used especially to investigate the presence of ENNs on leaflets blade, and on bracts and petals.

RESULTS

Extranuptial nectaries in *Carapa*

ENNs in *Carapa* include extrafloral nectaries (EFNs) on leaves (several locations), petaline nectaries on flowers and pericarpial nectaries in fruits (Fig. 2).

Extrafloral nectaries

EFNs are all foliar, located on the petiole, rachis, and leaflet blades of the pinnately compound leaf. Petiolar nectaries occur on the abaxial surface of the swollen base of the petiole in 23 (85%) of the *Carapa* species examined. Their morphology (categories following Zimmermann [1932]) varies among species, from pit (Fig. 1E) to flattened (Fig. 2D) or elevated (Fig. 1G). Petiolar nectaries are conspicuous in only a few species, and most notably so on petioles of young developing leaves. Petiolar nectaries are not present in all the leaves of an individual plant. When present, these nectaries range in number from 1 to 36 per petiole, with a mean among all individuals (without regard of species) of 3.4 (± 5.4). In most species, only two nectaries are present on each petiole, located on opposite sides (Fig. 1D). When more than two nectaries are present, they are irregularly distributed all over the base of the petiole (Fig. 1E, F). *Carapa macrantha* (Fig. 1F) has the highest mean number of petiolar nectaries (17 ± 11.5), followed by *C. parviflora* Harms (Fig. 1E) with a mean of 13 ± 10.6 and *C. dinklagei* Harms with a mean 4 ± 2 nectaries per petiole. These species also have the highest mean number of leaflets. Indeed, counts on 241 leaves belonging to all 27 species of *Carapa* show that there is a positive correlation ($y = 0.4304x - 4.034$, $R^2 = 0.4232$) between the mean number of leaflets (y) and the mean number of petiolar nectaries (x) per species. Petiolar nectaries also occur at the base of the modified scale-like leaves that subtend the inflorescence (Fig. 1H, I).

Nectaries on the rachis are flat and located on the abaxial surface and at the base of the petiolules (Fig. 2A, B). There is generally one at the base of the petiolule of each leaflet. However, field observations on fresh material show that nectaries may not occur at the base of all leaflets.

Almost all *Carapa* leaflets examined bear numerous EFNs on their abaxial surface, especially along the midrib and secondary veins. These nectaries are tiny, ellipsoid and flattened, and are only visible under a dissecting microscope. The apices of the leaflets in some species of *Carapa* have glandular mucros that are active in very immature leaflets and dry up when the leaflets reach maturity (Fig. 2E).

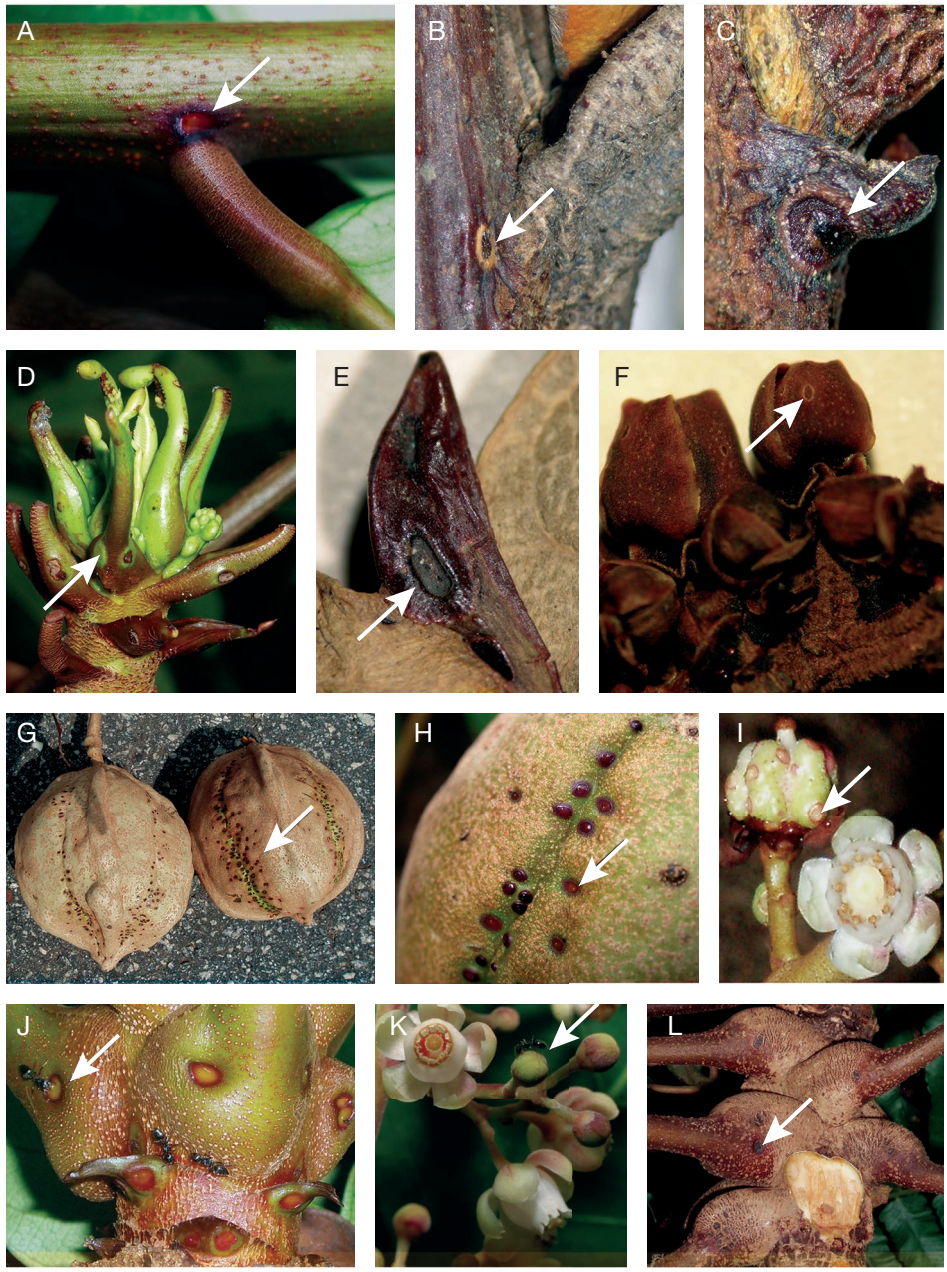

Fig. 2 — Extrafloral nectaries in *Carapa*: **A**, **B**, rachis nectary in *C. littoralis* Kenfack near Limbe, Cameroon (**A**) and a dried specimen (*Kenfack 2068*, MO) of *C. macrantha* Harms from Lalara-Alembe road, Gabon (**B**); **C**, bract nectary in a dried specimen (*Kenfack 2067*, MO) of *C. macrantha* from near Makokou, Gabon; **D**, **E**, mucro nectary on living and dried specimen (*Kenfack 2067*, MO) of *C. macrantha*; **F**, petaline nectary on a dried specimen (*Vasquez & Jaramillo 4827*, MO) of *C. vasquezii* Kenfack from Loreto, Peru; **G**, **H**, fruit nectaries in *C. procera* C.DC. from Ejura, Ghana (**G**) and Mali (**H**); **I**, fruit nectaries on a young fruit of *C. zemagoana* Kenfack from Mokoko, Cameroon; **J**, **K**, ants foraging on exudate from petiolar (**J**) and petal (**K**) nectaries in *C. microcarpa* A. Chev. from Sagymaase, Ghana and *C. procera* from Mali, respectively; **L**, dried petiolar nectaries in *C. microcarpa* from Sagymaase, Ghana.

Glandular mucros are absent in a few taxa (*C. angustifolia* Harms, *C. planadensis* Kenfack, *C. alticola* Kenfack & Peréz, *C. oreophila* Kenfack), interestingly, all of which grow at higher elevations (600-2500 m).

Bracts subtending inflorescence branches or flowers generally have a single conspicuous nectary on their abaxial surfaces (Fig. 2C). These nectaries are absent in a few species of *Carapa* (Table 1).

Pericarpial nectaries

ENNs also occur on the surface of fruits, mostly grouped on the exocarp towards the carpel boundaries (Fig. 2G, H). Fifty-seven percent of the species of *Carapa* examined have these fruit nectaries also called pericarpial nectaries (Table 1). They are present and particularly conspicuous in young immature fruits (Fig. 2I). Indeed, careful examination of the ovary of a few species, using a dissecting microscope, revealed the presence of pit nectaries on the surface of the ovary. Pericarpial nectaries generally occur in large numbers. We recorded in average 742 ±78 (mean ± SD) nectaries on the surfaces of five fruits (each *c.* 15 × 9 cm) of *C. procera* C.DC. collected from a gallery forest in Ghana. *Petaline nectaries* – Flat nectaries occur on the median region of the abaxial surface of the petals, near the apex (Fig. 2F). These are often referred to as petaline nectaries. They are only visible under a dissecting microscope. Generally, each petal bears only a single nectary.

Geographic distribution of extranuptial nectaries

ENNs occurred in *Carapa* throughout its distributional range in Africa and the Neotropics. On average, African species have more petiolar nectaries than American species. For example in average, African species had 4 (±7.3) petiolar nectaries while American species had only 1.8 (±0.4). Species without petiolar nectaries (most of which grow at higher elevation) occur in both regions.

Activity of extranuptial nectaries and of ants

Active nectar secretion by ENNS in *Carapa* is generally limited to young developing organs. For example, in all Neotropical and a few of African species observed, petiolar ENNs were active only in the early stages of leaf development (Fig. 1D, G); in mature leaves they ceased secretion and were reduced to inconspicuous black spots at the base of the petiole (Fig. 2L). Petaline nectaries are active and attract ants in the flower bud stage (Fig. 2K). However, we noted that nectary activity varies among species and organs. In some African species, such as *Carapa macrantha* and *C. parviflora*, petiolar nectaries remain active on fully developed, mature leaves (Fig. 1E, F), generally attracting a wide variety of arthropods, especially ant species (Figs 1I; 2J). For example, in Senegal we recorded four species of ants on *C. velutina* C.DC. near the Dindefelo waterfall (*Oecophylla longinoda* Latreille, and unidentified species of *Cataulacus* F. Smith, *Crematogaster* Lund and *Camponotus* Mayr), while three species were found on *C. procera* in Casamance (*Oecophylla longinoda* Latreille and unidentified species of *Camponotus* and *Crematogaster*).

Extranuptial nectaries in other Cedreloideae

To investigate the potential taxonomic value of ENNs, we expanded our investigation to the remaining 13 genera of subfamily Cedreloideae. The results show that most of the EFN types observed in *Carapa* are not unique to the genus (Table 1). From our sample, lamina nectaries appear to be very common in the subfamily, whereas mucronal, bracteal, petaline and pericarpial nectaries are restricted to only a few genera.

DISCUSSION

We report here for the first time the presence of ENNs at the base of the petiole, on the rachis, the bracts, the petals and the fruits in *Carapa*. To date, the only reports of ENNs in the genus were those of Zimmermann (1932), who recorded nectaries on the lower surface of the leaf of two members of the genus, *C. guianensis* Aubl. and *C. moluccensis* (the latter now regarded as a synonym of *Xylocarpus moluccensis* (Lam.) M. Roem.), and of Baillon (1875), who reported nectaries at the apex of leaflets. Zimmermann (1932) also noted the presence of "elongate dark flecks of doubtful func-

TABLE 1. — Distribution of nectaries on several plant organs in *Carapa* Aubl. and 13 other genera of Meliaceae, subfamily Cedreloideae. Abbreviations: **+**, present; **–**, absent; **?**, not investigated.

Species name	Field/Herbarium study	Petiole base	Rachis	Reduced leaves	Lamina	Mucro	Bract	petals	Fruit surface
Carapa angustifolia Harms	Mt Kupe, Cameroon	–	–	–	+	–	–	+	–
Carapa batesii C.DC.	Herbarium	+	+	–	+	–	+	+	+
Carapa dinklagei Harms	Korup, Cameroon	+	+	+	–	+	+	+	+
Carapa gogo A. Chev. ex Kenfack	Herbarium	+	–	+	+	–	+	+	+
Carapa grandiflora Sprague	Herbarium	+	–	+	+	+	+	+	–
Carapa hygrophila Harms	Africa	+	+	+	+	+	+	+	+
Carapa littoralis Kenfack	Debundsha, Cameroon	+	+	+	+	+	+	+	–
Carapa macrantha Harms	Makoku, Gabon	+	+	+	+	+	+	+	+
Carapa mangarevensis Kenfack & Issembe	Oveng, Gabon	+	+	+	–	+	+	+	?
Carapa microcarpa A. Chev.	Sagymaase, Ghana	+	–	+	+	+	+	+	+
Carapa oreophila Kenfack	Mt Kupe, Cameroon	+	–	–	+	+	–	–	?
Carapa palustris (G. Gilbert) Kenfack	Abignam, Cameroon	+	+	+	+	+	+	+	–
Carapa parviflora Harms	Korup, Cameroon	+	+	+	+	+	+	+	+
Carapa procera C.DC.	Ejura, Ghana	+	–	+	+	+	+	+	+
Carapa velutina C.DC.	Thionk-Essyl, Senegal	+	–	+	+	+	+	+	+
Carapa zemagoana Kenfack	Diongo, Cameroon	+	–	+	+	+	+	–	+
Carapa akuri Poncy, Forget & Kenfack	Iwokrama, Guyana	+	–	+	+	+	+	+	+
Carapa alticola Kenfack & Peréz	Reserva Endesa, Ecuador	+	–	+	+	–	–	+	–
Carapa guianensis Aubl.	Barima river, Guyana	+	+	+	+	+	+	+	+
Carapa llanocarti Kenfack	Nusagandi, Panama	–	–	+	+	+	+	+	?
Carapa longipetala Kenfack	Reserva Awá, Ecuador	+	–	+	+	+	–	+	–
Carapa megistocarapa A.H. Gentry & Dodson	Reserva Endesa, Ecuador	+	–	–	+	–	–	–	–
Carapa vasquezii Kenfack	Herbarium	+	+	+	+	+	+	+	+
Carapa nicaraguensis C. DC.	San Lorenzo, Panama	+	+	+	+	+	–	+	–
Carapa pariensis Kenfack	Herbarium	–	–	–	+	–	–	–	–
Carapa planadensis Kenfack	Herbarium	–	–	–	–	–	–	–	–
Carapa surinamensis Miq.	Herbarium	+	+	+	+	+	+	+	+
Capuronianthus mahafalensis J.-F. Leroy	Herbarium	–	–	–	–	–	–	–	?
Capuronianthus vohemarensis J.-F. Leroy	Herbarium	–	–	–	–	–	–	–	–
Cedrela angustifolia Moc. & Sessé ex DC.	Herbarium	–	+	–	+	–	–	–	–
Cedrela fissilis Vell.	Herbarium	–	+	–	–	–	–	–	–
Cedrela odorata L.	Herbarium	–	+	–	+	–	–	–	–
Chukrasia tabularis var. *velutina* King	Herbarium	+	+	–	+	–	–	–	–
Entandrophragma angolense var. *macrophyllum*	Herbarium	–	–	+	+	–	–	–	–
Entandrophragma candollei Harms	Herbarium	–	–	–	+	–	?	?	?
Entandrophragma caudatum (Sprague) Sprague	Herbarium	–	+	–	+	–	–	–	–
Entandrophragma cylindricum Sprague	Herbarium	–	+	–	+	–	–	–	–
Khaya grandifoliola C. DC.	Herbarium	+	–	+	+	?	–	+	?
Khaya ivorensis A. Chev.	Herbarium	+	–	+	+	–	–	+	–
Khaya senegalensis (Desr.) A. Juss.	Herbarium	+	–	+	+	–	+	+	–
Lovoa trichilioides Harms	Herbarium	–	+	–	+	–	–	–	–
Neobeguea mahafaliensis J.-F. Leroy	Herbarium	–	+	–	+	–	–	–	–
Pseudocedrela kotschyi (Schweinf.) Harms	Ejura, Ghana	–	+	–	+	–	–	–	–
Schmardaea microphylla (Hook.) H. Karst. ex Müll. Hal.	Herbarium	+	+	–	–	–	–	–	–
Soymida febrifuga (Roxb.) A. Juss.	Herbarium	–	–	–	+	–	–	+	+
Swietenia macrophylla King	Panama City, Panama	+	+	–	+	–	–	+	–
Toona ciliata M. Roem.	Herbarium	+	+	–	+	–	–	–	–
Toona phylippinensis Elm	Herbarium	–	+	–	+	–	–	–	–
Xylocarpus granatum J. Koenig	Herbarium	+	–	–	+	–	–	+	–
Xylocarpus moluccensis (Lam.) M. Roem.	Herbarium	–	+	–	+		–	+	–

tion" (see Lersten & Rugenstein 1982) at the base of the petiole of *C. guianensis*, which we confirm here to be petiolar nectaries. This author probably examined only mature leaves, on which nectaries had ceased to secrete.

Foliar nectaries, especially petiolar, were the most common. They were senescent in some species at maturity but in the majority of the species of *Carapa*, they seemed to be functional during the whole lifespan of the leaf, as in another *Cedrela fissilis* Vell. (Meliaceae) (Paiva *et al.* 2007). Foliar nectaries were observed in young and mature leaves of adult trees, but we failed to check their presence in seedlings and saplings. In some tropical tree species such as *Sacoglottis* sp. (Humiriaceae) and *Anthocleista nobilis* G. Don (Gentianaceae), foliar nectaries develop early in their ontogeny (Belin-Depoux 1993). The number of foliar nectaries was positively correlated to the number of leaflet (thus leaf surface), suggesting that in *Carapa*, if the nectaries are proven to be effective in protecting individual plants from herbivores, more nectaries are required to protect large-leaved species.

Petaline nectaries were found in five genera of Cedreloideae. Within Melioideae, they have been reported only in *Trichilia havanensis* Jacq. (Díaz-Castestelazo *et al.* 2004). They are less common outside of Meliaceae. Petaline nectaries in *Swietenia macrophylla* King (Meliaceae) secrete nectar from buds to full anthesis of the flowers (Paiva 2011). In *Carapa*, petaline nectaries are also active in flower buds and are known to attract ants (Fig. 2K).

Our finding of nectaries on *Carapa* fruits is only the second record of nectaries in fruits for Meliaceae and even the order Sapindales, the only other being in *Guarea macrophylla* Vahl (Morellato & Oliveira 1994). Pericarpial nectaries in *Carapa* develop early in flowers and appear to secrete at anthesis (Kenfack pers. obs.), they may thus reward pollinators in their early stage of development. Such nectaries that play a role in pollination and continue to function in developing fruits have been termed postfloral nectaries (Daumann 1932; Bentley 1977, Keeler 1981).

EFNs in *Carapa* are inconspicuous in most species, particularly in mature plant parts, and even more so in dried specimens. This fact might explain why taxonomists have failed to report them in the past. Of the more than 1300 herbarium specimens examined in the course of the revision of *Carapa*, the only mention of nectaries on labels was from a recent collection of *C. macrantha* (*Wieringa* 6355) from Gabon. The collector stated "…at the base of the spines [reduced scale-like leaves], one finds c. 10 glands that probably feed the ants". Identifying ENNs on herbarium specimens was facilitated by the fact that we first observed them on living specimens in the field.

Carapa species growing at comparatively high elevations have few if any ENNs. In fact, the frequency of plant species with ENNs is inversely correlated with elevation (Keeler 1979).

Although ENNs are also present in other Meliaceae, we suggest that their presence in particular on the leaflet mucro, bracts, petals and fruits can be used, both on living or dried specimens, as a character for the identification of *Carapa* species. For example, *C. macrantha*, *C. parviflora* and *C. dinklagei* can easily be distinguished from other taxa of the genus (and perhaps of the family) by the presence of numerous nectaries on their petiole.

ENNs in *Carapa* secrete a sweet liquid (Kenfack pers. obs.) which attracts a diverse community of ants. This might explain, at least in part, the abundance of ants on *Carapa* trees.

The benefits that ENNs confer on plants are not always obvious, but evidence has been provided for protection by ants opportunistically attracted to plant-derived rewards (Costa *et al.* 1992; del Claro *et al.* 1996; Koptur *et al.* 1998; de la Fuente & Marquis 1999; Oliveira *et al.* 1999; Sobrinho *et al.* 2002). As in other myrmecophilous plants (Keeler 1980; Costa *et al.* 1992; Belin-Depoux 1993, Sobrinho *et al.* 2002; Katayama & Suzuki 2005; Leal *et al.* 2006), the presence of ENNs in *Carapa* trees – including postfloral nectaries – may confer fitness benefits. For example in *Mentzelia nuda* (Pursh) Torr. & A. Gray (Loasaceae), nectar produced by postfloral nectaries attracts ants and their presence enhances seed set (Keeler 1981). The effectiveness of nectaries in protecting plants against herbivores depends on their location and their number. Plants with more nectaries produce more nectar, attract a larger ant community and deter better herbivores. For example in *Anthocleista*

nobilis G. Don (Gentianaceae) each leaf has tens of laminar glands and about ten petiolar nectaries that confer to this species a good protection against herbivores (Belin-Depoux 1993). In this respect, *Carapa macrantha*, *C. parviflora* and *C. dinklagei* with the highest number of nectaries are the best equipped to protect these species against herbivores. Further field investigations will be needed to inventory ants and other arthropod communities on *Carapa* trees and to determine the nature of their relationship with these plants.

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Appendix. — Supporting online material: selected specimens examined.

Carapa akuri Poncy, Forget & Kenfack

MATERIAL EXAMINED. — **Guyana**. *D. Kenfack et al. 2108* (MO); *D. Kenfack et al. 2109* (MO); *P. Acedevo 3431* (MO); *P. Mutchnick & B. Allicock 383* (MO); *P.M. Forget 501* (MO); *P.M. Forget 502* (MO); *R.C. Ek. M. Williams & A Williams 624* (MO); *S. Tiwari 437* (MO).

Carapa alticola Kenfack & Peréz

MATERIAL EXAMINED. — **Ecuador**. *D. Kenfack 2155* (MO); *D. Neil & QCNE 12736* (MO); *J. Jaramillo 6970* (MO); *J. Jaramillo 7039* (MO); *W. Palacios et al. 9689* (MO).

Carapa angustifolia Harms

MATERIAL EXAMINED. — **Cameroon**. *D. Kenfack* 2007 (MO); *S. Moses* 318 (MO).

Carapa batesii C.DC.

MATERIAL EXAMINED. — **Cameroon**. *A.J.M. Leeuwenberg 6397* (WAG); *G.L. Bates 535* (MO); *P. Tchouto 2963* (MO); *P. Tchouto et al. 3414* (WAG); *R. Letouzey 1289* (MO).

Carapa dinklagei Harms

MATERIAL EXAMINED. — **Cameroon**. *A.J.M. Leeuwenberg 5279* (MO); *R. Letouzey 14950* (MO); *A. Binuyo 45466* (MO); *A.S. Jhoneuill 220* (MO); *D. Kenfack 1024* (MO); *D. Kenfack 1169* (MO); *D. Kenfack 1170* (MO); *D. Kenfack 1364* (MO); *D. Kenfack 1656* (MO); *D. Kenfack 2118* (MO); *D. Kenfack 737* (MO); *D.W. Thomas & J. Nemba 5932* (MO); *D.W. Thomas 2352* (MO); *D.W. Thomas 8256* (MO); *G. Zenker 145* (MO); *G. Zenker 3713* (MO); *G. Zenker sn* (MO); *J.J. Bos 4374* (MO); *M. Akogo 174* (MO); *Mainoud 430* (MO); *T.D. Maitland 431* (MO). — **Equatorial Guinea**. *M.F. de Carvalho 2252* (MO); Gabon. *C. Barter 153* (MO). — **Nigeria**. *P.A. Talbot 1462* (MO); *P.W. Richards 3013* (MO); *G. Mann 1767* (MO).

Carapa gogo A. Chev. ex Kenfack

MATERIAL EXAMINED. — **Sao Tome**. *A. Chevalier 14503* (MO); *Groenendijk 24* (WAG); *L. Groenendijk 31* (WAG); *Groenendijk 35* (WA); *L. Groenendijk 47* (WAG).

Carapa grandiflora Sprague

MATERIAL EXAMINED. — **Burundi**. *P. Auguier 4186* (MO). — **Rwanda**. *G. Bouxin 925* (MO); *P.M. Forget & A. Nyiramema 581* (MO). — **Tanzania**. *J. Kahuramanga 2565* (MO). — **Uganda**. *B.T. Styles 20* (MO).

Carapa guianensis Aubl.

MATERIAL EXAMINED. — **Brazil**. *B. Nelson 803* (MO); *B.A. Krukoff 1048* (MO); *B.A. Krukoff 4776* (MO); *B.A. Krukoff 8120* (MO); *B.V. Rabelo & J. Cardoso 2886* (MO); *B.V. Rabelo et al. 1865* (MO); *B.V. Rabelo et al. 2349* (MO); *D.C. Daly et al. 3906* (MO); *Duke 410* (MO); *G.T. Prance & T.D. Pennington 1990* (MO); *G.T. Prance & T.D. Pennington 1255* (MO); *G.T. Prance et al. 1378* (MO); *G.T. Prance et al. 1644* (MO); *J. Ramos 920* (MO); *N.T. Silva & U. Brazão 60674* (MO); *R. Froes & B.A. Krukoff 11706* (MO); *T.D. Pennington et al. 9964* (MO). — **Colombia**. *H.P. Fuchs & L. Zanella 21879* (MO); *M. M. Amaya & R. Vasques 188* (MO). — **Dominica**. *J. Higgins & P. Paris 127A* (MO); *W.H. & B.H. Hodge 3332* (MO). — **French Guiana**. *T. Granville 1093* (MO); *Oldeman 1027* (MO). — **Grenada**. *P. Beard 1296* (MO). — **Guatemala**. *H. Johnson 1195* (MO); Guyana. *A.S. Hitchcock 17524* (MO); *J.S. De la Cruz 4153* (MO); *W. Halm & S. Tiwari 5199* (MO). — **Honduras**. *A. Clewell & G. Cruz 4038* (MO). — **Nicaragua**. *A. Grijalva 6* (MO). — **Panama**. *C. Galdames et al. 3764* (MO). — **Peru**. *A. Gentry et al. 27498* (MO); *J. Pipoly et al. 13353* (MO); *R. Vásquez & N. Jaramillo 12708* (MO); *R. Vásquez & N. Jaramillo 2728* (MO). — **Venezuela**. *A. Castillo 708* (MO); *Bernardi 2123* (MO); *E.L. Little Jr. 17661* (MO); *F.J. Breteler 4947* (MO); *F.J. Breteler 5063* (MO); *J.A. Steyermark 87712* (MO); *J.J. Wurdack 292* (MO).

Carapa hygrophila Harms

MATERIAL EXAMINED. — **Cameroon**. *A. Chevalier 27115* (MO); *D. Kenfack & L. Zapfack 2035* (MO); *R. Letouzey 3901* (MO); *W. J.J.O. de Wilde & B.E.E. de Wilde-Duyfjes 2765* (MO). — **Gabon**. *A. Chevalier 27116* (MO).

Carapa littoralis Kenfack

MATERIAL EXAMINED. — **Cameroon**. *D. Kenfack 1365* (MO); *D. Kenfack 2106* (MO); *D. Kenfack & M.N. Sainge 2000* (MO); *D. Kenfack & M.N. Sainge 2001* (MO); *D. Kenfack & M.N. Sainge 2002* (MO); *D. Kenfack et al. 2107* (MO).

Carapa llanocarti Kenfack

MATERIAL EXAMINED. — **Panama**. *G. de Nevers et al. 4968* (MO); *M.D.A. Correa & R.L. Dressler 1115* (MO).

Carapa longipetala Kenfack

MATERIAL EXAMINED. — **Ecuador**. *C. Aulestia et al. 105* (MO); *C. Aulestia et al. 227* (MO); *D. Kenfack 2159* (MO); *H. van der Werff et al. 9501* (MO); *M. Tirado et al. 287* (MO).

Carapa macrantha Harms

MATERIAL EXAMINED. — **Democratic Republic of Congo**. *A. Masanga 17* (MO); *E.N. Ewango 1114* (MO); *J. Lebrun 5869* (MO). — **Gabon**. *A. Chevalier 27117* (MO); *D. Kenfack 2065* (MO); *D. Kenfack 2067* (MO); *D. Kenfack 2068* (MO); *D. Kenfack & N. Elias 1356* (MO).

Carapa mangarevensis Kenfack & Issembe

MATERIAL EXAMINED. — **Gabon**. *D. Kenfack 2050* (MO); *D. Kenfack 2051* (MO); *D. Kenfack 2052* (MO).

Carapa megistocarapa A.H. Gentry & Dodson

MATERIAL EXAMINED. — **Ecuador**. *C. Aulestia et al. 46* (MO); *C. Dodson et al. 14492* (MO); H. *van der Werff et al. 12377* (MO); *H. van der Werff et al. 9501* (MO); *H. Vargas et al. 1370* (MO); *W. Palacios & E. Freire 7430* (MO).

Carapa microcarpa A. Chev.

MATERIAL EXAMINED. — **Benin**. *C. Barter 3248* (MO). — **Ghana**. *A.A. Enti 613* (MO); *C. Vigne 2525* (MO); *Hutchinson 146* (MO); *J. Deaw 380* (MO); *J.J. Chipp 262* (MO); *J.K. Morton 25327* (MO); *N.H. Jhonson 146* (MO). — **Ivory Coast**. *A. Chevalier 16233* (MO); *A. Chevalier B. 22279* (MO); *J.J.F.E. de Wilde 3120* (MO); *Martineau 303* (MO). — **Nigeria**. *J.M. Dalziel 342* (MO).

Carapa nicaraguensis C. DC.

MATERIAL EXAMINED. — **Colombia**. *J. Espina, F. Garcia & S. Pino 2882* (MO). — **Costa Rica**. *A. Estrada et al. 989* (MO); *A.R. Molina et al. 17674* (MO); *B. Hammel et al. 18148* (MO); *C. Kerman & P. Phillips 893* (MO); *Fco. Queseda & M.M. Chavarria 392* (MO); *J.M. Orozco 492* (MO); *P.C. Stanley & J. Valerio 52493* (MO); *P.H. Allen 6718* (MO); *W. Burger & G. Matta U. 4716* (MO). — **Ecuador**. *C. Jativa & C. Epling 1113* (MO). — **Nicaragua**. *F.C. Englesing H-F572562* (MO); *J. C. Sandino 4511* (MO); *J. C. Sandino 4935* (MO); *J.C. Sandino 4740* (MO); *M. Nee 27837* (MO); *P.P. Moreno 25494* (MO). — **Panama**. *D. Kenfack 2005* (MO); *E.A. Lao, L.R. Holdridge 239* (MO); *F.C. García & E.D. Agualimpia 420* (MO); *G.P. Cooper & G.M. Slater 59* (MO); *I.M. Johnston 1824* (MO); *W.L. Stern et al. 969* (MO).

Carapa oreophila Kenfack

MATERIAL EXAMINED. — **Cameroon**. *R. Letouzey 14560* (MO); *D. Maitland 1663* (MO); *D.W. Thomas 5489* (MO); *L. Zapfack 1145* (MO); *M. Etuge 3452* (MO); *M.N. Sainge 1602* (MO); *M. Sainge 1261* (MO). — **Nigeria**. J.*D. Chapman 4354* (MO).

Carapa palustris (G. Gilbert) Kenfack

MATERIAL EXAMINED. — **Cameroon**. *G. Le Testu 4395* (MO); *R. Letouzey 3901* (MO); *R. Letouzey 4525* (MO). — **Democratic Republic of Congo**. *J. Lebrun 1245* (MO); *J. Louis 11935* (MO).

Carapa pariensis Kenfack

MATERIAL EXAMINED. — **Venezuela**. *D. Guerit & A.C. Gonzáles 19434* (MO); *G. Davidse & A. C. González 16603* (MO); *J.A. Steyermark & G. Agostini 91357* (US); *J.A.*

Steyermark & R. Liesner 120646 (MO); *J.A. Steyermark & R. Liesner 120874* (K, MO); *J.A. Steyermark 106256* (MO); *J.A. Steyermark 61338* (F, US); *J.A. Steyermark 62170* (US); *J.A. Steyermark 95095* (MO); *K. Dumont et al. VE-7589* (NY).

Carapa parviflora Harms

MATERIAL EXAMINED. — **Cameroon**. *J.J.F.E. de Wilde 7477* (MO); *D. Kenfack 1087* (MO); *D. Kenfack 1165* (MO); *D. Kenfack 1166* (MO); *D.W. Thomas 4782* (MO); *F.J. Breteler et al. 2583* (MO); *J.J. Bos 2989* (MO); *M.N. Sainge 378* (MO); *P. Tchouto 3196* (MO); *R. Letouzey 10155* (MO); *T.R. van Andel et al. 4116* (MO). — **Central African Republics**. *D.J. Harris & J.M. Fay 1953* (MO). — **Gabon**. *D. Kenfack 2053* (MO); *D. Kenfack 2057* (MO); *D. Kenfack 2060* (MO); *D. Kenfack 2066* (MO); *F.J. Breteler & M.E. Leal 14256* (MO); *J.M. & B. Reitsma 1321* (MO); *J.M. & B. Reitsma 1321* (MO); *L. White 1053* (MO); *L. White 1532* (MO); *R.P. Klaine 549* (MO).

Carapa planadensis Kenfack

MATERIAL EXAMINED. — **Colombia**. *A. Gentry 35056* (MO); *A. Gentry et al. 30546* (MO); *P. Franco, et al. 4960* (MO); *W. Palacios et al. 9689* (MO).

Carapa procera C.DC.

MATERIAL EXAMINED. — **Ghana**. *D. Kenfack & J. Amponsah 2091* (MO); *H.H. Schmidt et al. 1958* (MO). — **Guinea**. *A. Chevalier 14865* (MO); *A. Chevalier 14869* (MO); *A. Chevalier 20474* (MO); *Cordonier 243* (MO); *F. Malaisse 2541* (MO). — **Liberia**. *A.G. Voorhoeve 1288* (MO); *D.H. Linder 1156* (MO); *D.H. Linder 905* (MO); *J.G. Adam 28702* (MO); *J.T. Baldwin Jr. 10284* (MO); *J.W.A. Jansen 1360* (MO). — **Senegal**. *A. Chevalier 3164* (MO); *Anonymus 3166* (MO); *D. Kenfack et al. 2076* (MO); *D. Kenfack et al. 2077* (MO); *D. Kenfack et al. 2080* (MO); *D. Kenfack et al. 2085* (MO); *Fotius K811* (MO); *Kaoussou Sambou, 1* (MO); *Kaoussou Sambou, T. Sarr sn* (MO); *Madsen J. E. 3123* (MO). — **Sierra Leone**. *C.E. Lane-Pook 349* (MO); *D. Cledhill 301* (MO); G.F. Scott Elliot 4153 (MO); *M. Heudelot 749* (MO).

Carapa surinamensis Miq.

MATERIAL EXAMINED. — **Brazil**. *G.T. Prance et al.* 23033 (MO); *T.D. Pennington et al. 9996* (MO). — **French Guiana**. *Cremers 5029* (MO); *M. Hoff 7189* (MO); *R. Benoist 286* (MO); *S. Mori & A. Bolten 8649* (MO); *S. Mori & B. Boom 15123* (MO); *S. Mori et al. 21528* (MO); *Sagot 979* (MO); *Sagot s.n.* (MO). — **Suriname**. *BBS 407* (MO); *G. Stahel 105* (MO); *H. Jimenez-Saa LBB14307* (MO); *R. Evans & S. Koemar 3181* (MO); *R. Evans et al. 2479* (MO); *SC 5566* (MO).

Carapa vasquezii Kenfack

MATERIAL EXAMINED. — **Brazil**. *B. Boom et al. 8609* (MO); *C.A. Cid et. 8536* (MO); *C.A. Cid Fereira et al. 9994* (MO); *G.T. Prance & J.F. Ramos 23551* (MO); *M.A.D. de Souza et al. 425* (MO); *P. Kukle 113* (MO); *R. Vásquez & N. Jaramillo 9243* (MO); *T.D. Pennington et al. 9931* (MO). — **Peru**. *R. Vasquez & N. Jaramillo 4827* (MO); *R. Vasquez & N. Jaramillo 963* (MO).

Carapa velutina C.DC.

MATERIAL EXAMINED. — **Guinea**. *A. Chevalier 18192* (MO); A. Chevalier 408 (MO); *A. Chevalier 461* (MO); *H. Pobéguin s.n.* (MO). — **Guinea-Bissau.** *E. Santo 1310* (MO). — **Ivory coast**. *H. Pobéguin 264* (MO); *L. Gautier et al. 2857* (MO). — **Mali**. M. R. Dubois 38 (MO). — **Senegal**. *D. Kenfack 2070* (MO); *D. Kenfack 2074* (MO); *D. Kenfack 2084* (MO); *D. Kenfack et al. 2071* (MO); *D. Kenfack et al. 2072* (MO); *D. Kenfack et al. 2079* (MO); *D. Kenfack et al. 2081* (MO); *D. Kenfack et al. 2083* (MO); *A. Goudiaby 1273* (MO); *J.-G. Adam 17514* (MO).

Carapa zemagoana Kenfack

MATERIAL EXAMINED. — **Cameroon**. *D. Kenfack 1508* (MO); *D. Kenfack 627B* (MO); *D. Kenfack 1368* (MO); *D. Kenfack 627* (MO); D. Kenfack *et al.* 2116 (MO); *J. Watts 632* (MO); *J.M. Mbani 379* (MO); *N. Ndam 1315* (MO); *P. Fraser 356* (MO). — **Nigeria**. *M.G. Latilo 29* (MO).

Cedrela fissilis Vell.

MATERIAL EXAMINED. — **Bolivia**. *A.F. Fuentes et al. 7896* (MO); *J.C. Solomon et al. 18966* (MO); *M. Serrano & C. Pérez 2683* (MO); *M.H. Nee 37834* (MO); *M.P. Saldías et al. 2950* (MO). — **Brazil**. *E.P. Heringer & G. Eiten 14991* (MO). — **Peru**. *D.S. Camilo 2525* (MO); *D.S. Camilo & M.S. Baldeón 2281* (MO); *P.V. Núñez et al. 11486* (MO).

Cedrela odorata L.

MATERIAL EXAMINED. — **Bolivia**. *D.N. Smith et al. 14295* (MO). — **Brazil**. *Carvalho 4130* (MO). — **Colombia**. *S. Alexandre & N. Paz 7573* (MO). — **Ecuador**. *C.E. Cerón et al. 425* (MO); *Z. Vlastimil 1219* (MO). — **Mexico**. *A.G. Rincón 1045* (MO). — **Nicaragua**. *A. Laguna 106* (MO); *D.A. Neill 492* (7344a) (MO); *M. Araquistain & P.P. Moreno 2824* (MO); *R.M. Rueda & L.D. Paguaga 13806* (MO); *W. Robleto T. 729* (MO); *W.D. Stevens & O.M. Montiel J. 17381* (MO). — **Panama**. *J.A. Duke 5231* (MO); *T.B. Croat 10332* (MO). — **Peru**. *Camilo Díaz S. & et al. 2501* (MO); *D.N. Smith 4178* (MO).

Chukrasia tabularis A. Juss.

MATERIAL EXAMINED. — **China**. *C. Wang 34114* (MO). — **Hong Kong**. *S. Liu 282* (MO); *S.Y. Hu & K.H. Yung 603* (MO).

Entandrophragma angolense (Welw. ex C. DC.) C. DC.

MATERIAL EXAMINED. — **Cameroon**. *D.W. Thomas 7699* (MO); *J. Nemba & D.W. Thomas 481* (MO). — **Central African Republic**. *D.J. Harris 4110* (MO); D.*J. Harris & J.M. Fay 1398* (MO); *D.J. Harris & J.M. Fay 1762* (MO); *J.M. Fay & D.J. Harris 8789* (MO). — **Democratic Republic of Congo**. *T.B. Hart 1125* (MO). — **Gabon**. *C. Wilks 1609* (MO). — **Nigeria**. *G.E. Pilz 2042* (MO).

Entandrophragma candollei Harms

MATERIAL EXAMINED. — **Cameroon**. *D.W. Thomas 8169* (MO); *D.W. Thomas & H.L. MacLeod 5873* (MO). — **Central African Republic**. *J.M. Fay & D.J. Harris 8493* (MO). — **Democratic Republic of Congo**. *J. Louis 13077* (MO); *J. Louis 2319* (MO).

Entandrophragma caudatum Sprague

MATERIAL EXAMINED. — **Zimbabwe**. *Torre et al. 18751* (MO); *D. Taylor s.n.* (MO).

Entandrophragma cylindricum (Sprague) Sprague

MATERIAL EXAMINED. — **Central African Republic**. *D.J. Harris & J.M. Fay 1880* (MO); *J.M. Fay & D.J. Harris 8557* (MO). — **Democratic Republic of Congo**. *T.B. Hart 1353* (MO). — **Gabon**. *G. Dauby GD 1323* (MO). — **Uganda**. *ATBP 667* (MO).

Khaya grandifoliola C. DC.

MATERIAL EXAMINED. — **Ghana**. *C.C.H. Jongkind 2318* (MO). — **Tanzania**. *D.K. Harder & R.E. Gereau 1385* (MO); *H.H. Schmidt 1196* (MO). — **Uganda**. *D.A.H. Taylor 230* (MO).

Khaya ivorensis A. Chev.

MATERIAL EXAMINED. — **Equatorial Guinea**. *Carvalho 3510* (MO). — **Gabon**. *G. Dauby GD 1282* (MO). — **Zimbabwe**. *R.D.A Bayliss 9014* (MO). — **Ivory Coast**. *L. Aké-Assi 18955* (MO).

Khaya senegalensis (Desr.) A. Juss.

MATERIAL EXAMINED. — **Cameroon**. D.W. Thomas 2053 (MO). — **Ghana**. *C. Jongkind et al. 1466* (MO); *C.C.H. Jongkind 2372* (MO). — **Nigeria**. *J.D. Chapman 4074* (MO). — **Senegal**. *L.F. Marchant et al. 19* (MO).

Lovoa trichilioides Harms

MATERIAL EXAMINED. — **Cameroon**. *A.J.M. Leuvemberg 5076* (MO). — **Central African Republic**. *J.M. Fay & D. J. Harris 8883* (MO). — **Democratic Republic of Congo**. P. Staner 1520 (MO). — **Gabon**. *R.P. Klaine s.n.* (MO). — **Liberia**. *J.W.A. Jansen 2080* (MO).

Pseudocedrela kotschyi (Schweinf.) Harms

MATERIAL EXAMINED. — **Ethiopia**. *R.E. Gereau 1337* (MO). — **Ghana**. *H.H. Schmidt et al. 1826* (MO). — **Senegal**. *A. Jacques-George 13740* (MO). — **Sudan**. *N. Mohamed Awad 419* (MO).

Schmardaea microphylla (Hook.) H. Karst. ex Müll. Hal.

MATERIAL EXAMINED. — **Colombia**. *J.L. Zarucchi et al. 5471* (MO). — **Ecuador**. *J. L. Jaramillo 10296* (QCA); *G. Lewis & P. Lozano 3034* (MO). — **Peru**. *A.A. Sagástegui et al. 15935* (MO); *F. Woytkowski 6949* (MO); *R. Vásquez et al. 20528* (MO); *C.S. Díaz et al. 3159A* (MO); *C.S. Díaz et al. 3162* (MO); *Kenfack & Quizpe 2162* (MO).

Soymida febrifuga (Roxb.) A. Juss.

MATERIAL EXAMINED. — **Sri Lanka**. *M. Jarasuriya 386* (MO); *W. Meijer 784* (MO).

Swietenia macrophylla King

MATERIAL EXAMINED. — **Bolivia**. *Jiménez 84* (MO); *T.J. Killeen et al. 2934* (MO). — **Costa Rica**. *J.F. Morales 2561* (MO); *J.F. Morales 6043* (MO). — **Ecuador**. *J. Zuleta 60* (MO). — **El Salvador**. *E.A. Sandoval & M. Sandoval 994* (MO). — **Mexico**. *E.Fco. C. Cabrera & H. de Cabrera* 2169 (MO). — **Nicaragua**. *R.M. Rueda et al. 1460* (MO). — **Panama**. *E.L. Tyson 7403* (MO).

Toona ciliata M. Roem

MATERIAL EXAMINED. — **India**. *Maharashtra 95811* (MO); *C. Saldanha 12057* (MO).

Xylocarpus granatum J. Koenig

MATERIAL EXAMINED. — **Madagascar**. *Rhelivololona 5* (MO); *S.F. (Capuron) 24325* (MO). — **New Caledonia**. *G. McPherson 5817* (MO).

Xylocarpus moluccensis (Lam.) M. Roem.

MATERIAL EXAMINED. — **Madagascar**. *F. Ratovoson 934* (MO). — **Tanzania**. *M. Mwangoka 3338* (MO).