THE BOTANICAL REVIEW

VOL. 63 OCTOBER–DECEMBER 1997 NO. 4

Chemistry of Cerambycid Host Plants. Part I: Survey of Leguminosae—A Study in Adaptive Radiation

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The Botanical Review 63(4) 356–394, October–December 1997

I. Abstract

Eighty wood samples representing 51 taxa in 33 genera of Leguminosae were collected in the Sinnamary River Basin in Northern French Guiana and evaluated for their fauna of long-horned beetles (Cerambycidae) and their phytochemical constituents. The cerambycid fauna was assessed using cut branches and trunks that were continuously observed for emerging beetles. Phytochemical patterns were determined in partially purified methanolic extracts that were obtained from wood and bark of the same branches and trunks using thin-layer chromatography (TLC) and high-pressure liquid chromatography (HPLC). It was found that small groups of taxonomically related and often phytochemically similar plant species serve as host plants for small and well-defined longicorn guilds. Members of longicorn guilds are usually not taxonomically related. Host-plant chemistry appears to play a role in resource allocation among longicorn guilds in this lowland neotropical rainforest. These findings are discussed in reference to theories on coevolution and adaptive radiation in plant–insect associations.

Zusammenfassung

Insgesamt achtzig Holzproben, die im Becken des Sinnamary im nördlichen Französisch Guiana von 51 Taxa der Leguminosen entnommen wurden und insgesamt 33 Gattungen repräsentieren, wurden in Hinblick auf ihre Langhornkäferfauna (Cerambycidae) und ihre phytochemischen Eigenschaften untersucht. Gefällte Stämme wurden über die Dauer von vier Monaten hinweg beobachtet, um die schlüpfenden Langhornkäfer zu identifizieren. Die phytochemischen Profile wurden mittels Dünnschichtchromatographie (DC) und Hochdruckflüssigkeitschromatographie (HPLC) von methanolischen Extrakten charakterisiert, die von den Holzproben der frisch gefällten Stämmen angefertigt wurden. Die Resultate dieser Untersuchung zeigen, dass kleinere Gruppen taxonomisch verwandter und oft phytochemisch ähnlicher Leguminosenarten als Wirtspflanzen für kleine, aber gut beschreibbare Langhornkäfersippen dienen. Die Arten dieser Langhornkäfersippen zeigen oft keinerlei taxonomische Verwandtschaft. Daher kann angenommen werden, dass die phytochemischen Profile der Wirtspflanzen eine wichtige Rolle in der Nutzung und Erkennung von potentiellen Wirtspflanzen in diesem tiefliegenden Neotropischen Regenwald spielen. Diese Resultate werden im Hinblick auf die Theorien der Coevolution und der adaptiven Kolonisierung von Wirtspflanzen diskutiert.

II. Introduction

Ever since Ehrlich and Raven's paper was published in 1964, the hypothesis of coevolution has received much attention. Their study directed attention for the first time to the role of plant chemistry in the interaction with insects. Many of the questions addressed in that paper, as well as the hypotheses put forward by Ehrlich and Raven, have since been subject to elaborately designed studies, but many questions remain. One of these questions is whether arthropods are the driving force behind a selection process that yields the enormous diversity of secondary metabolites that we see in the plants dominating the earth's ecosystems today.

The idea of the one-to-one reciprocal evolution scheme between arthropods and their respective host plants was read into Ehrlich and Raven's paper (we believe that they themselves were much more conservative in their conclusions) and proven to be indefensible (Thompson, 1988). Parallel cladogenesis on the species level between insects and their host plants has really been documented in only very few instances (Farrell & Mitter, 1990), and in no case have the chemical components involved in these associations been investigated. A theory labeled "diffuse coevolution," proposed by Fox (1988), states that the diversity of plant chemicals has evolved in concert with a multitude of past herbivores and pathogens. The theory states that many species, on the same or different trophic levels, may simultaneously exert selective pressures on one another and be affected by changes in other component members of the system. This includes changes in plant chemicals (Fox, 1988; reply to Bernays & Graham, 1988). The theory of "diffuse coevolution" also specifically includes the role that microbial infestations may play in the evolution of secondary plant metabolites. Thompson (1988) recognizes that interactions between insects and plants are one of the most diverse associations between taxa in terrestrial communities, and that specificity in these interactions is unlikely to have one single major cause.

However, the difficulty in measuring evolutionary responses in plant chemistry has led to much frustration. Most studies conducted in this field have tried to prove that there is indeed a reciprocal interaction between herbivorous insects and their host plants (Berenbaum, 1983; Bowers, 1988, and references cited therein). While it seems possible to prove that insects may adapt to changes in the chemistry of host plants rather quickly (Renwick, 1988, and references cited therein; Bowers, 1988), it has not been proven that altered herbivore pressure results in changed chemical patterns of host plants, such as the production of new compounds, a change in profiles of existing compounds, or the omission just of stimulatory compounds. Admittedly, there are many observations and studies that support the defensive nature of many plant chemicals, and we have no intention of arguing against defense being their raison d'être. However, no experimental proof has been obtained to show that the occurrence of a single new herbivore or pathogen has actually favored an inheritable change in secondary metabolite composition in a plant. As a result of this lack of evidence, the role of plant chemistry in the evolution of insects has been questioned altogether: Bernays and Graham's (1988) major argument against chemical coevolution (that term here meaning that there is indeed a response in plant chemistry to changes in herbivore patterns on an evolutionary time scale) is that insects are generally rare on plants and, therefore, seldom exert much selection pressure on their hosts. This fact could also be a result of chemical defenses that plants evolved in the past, and the entire argument equates commonness of an interaction with intensity of selection (Thompson, 1988; reply to Bernays & Graham, 1988).

Brown (1987; Drummond & Brown, 1987) puts forward evidence that plant chemistry may play a role in resource allocation among different butterfly species but that the element of evolution of novel plant chemicals in response to predation by insect herbivores is certainly questionable. The present patterns of host utilization may be entirely the result of a process that Brown (1987) named "adaptive radiation." Applied to Brown's objects of study, the Ithomiinae, this means that these butterflies colonized their present solanaceous larval host plants long after their distinctive pattern of secondary metabolites had evolved. Chemistry appears to be used in host recognition, but most likely did not evolve in response to herbivore pressure by the butterfly larvae.

The study presented in this paper offers an entirely different perspective on insect–plant interactions. Instead of trying to demonstrate that changes in insect herbivory are responsible for changes in chemical profiles in plants over evolutionarily relevant periods of time, our study offers the unique opportunity to investigate a plant–herbivore interaction in which this kind of reciprocal response can definitely be excluded. The host plants of the cerambycid species investigated in the massive study in the Sinnamary River Basin in Northern French Guiana are dead at the time when the herbivory (e.g., oviposition and larval stages) occurs (Hequet & Tavakilian, 1996; Tavakilian et al., this issue). Therefore, existing patterns of host specificity in cerambycids cannot be explained with the theory of coevolution, not even "diffuse coevolution." Instead, this system can be studied with focus on adaptive responses necessary for colonizing a large group of host plants, a process Brown named "adaptive radiation" (1987). Phytochemical patterns of cerambycid host plants were analyzed to find correlations between patterns of host utilization and host chemistry. This provides circumstantial evidence that (1) long-horned beetles do recognize their host plants using chemical cues and (2) present patterns of host-plant utilization by arthropods may have emerged (at least in the case of the xylophagous longicorns of Sinnamary) through adaption to preexisting host-plant chemistry. (3) The results of this study allow us to compare patterns of host utiliziation that are known from organisms utilizing living host plants, e.g., plants with the potential of passing on potentially favorable chemical traits to their daughter generations.

The host plants of neotropical Cerambycid species have been the subject of a massive study conducted in the Sinnamary River Basin in Northern French Guiana (Hequet & Tavakilian, 1996; Tavakilian et al., this issue). A portion of this river basin was flooded in fall 1993 due to the construction of a dam. Prior to the flooding, a number of comprehensive studies on the flora and fauna of this pristine neotropical lowland rain forest were undertaken. In 1991–1993, approximately 600 trees were studied for their Cerambycid fauna, and more than 400 new plant-host relationships were discovered, along with a considerable number of longicorn species new to science. The cerambycid species will be described in a forthcoming monograph (Tavakilian, in prep.). In addition to the well-documented beetle fauna, this study also permitted the collection of plant species. During the 1992 and 1993 field seasons, wood samples of the prospective host plants were collected for phytochemical investigations. Of these collections, the Leguminosae were selected for a first phytochemical survey, because ample reference literature has recently become available which aided in the tentative identification of chemical compounds (Bisby et al., 1994; Hegnauer, 1994; NAPRALERT database). The legumes constitute the most abundant group of tropical trees in this area in terms of both numbers of individuals and numbers of species. This is matched only by the families Sapotaceae and Lecythidaceae. The Leguminosae of this area have been subject to a floristic treatment allowing for the proper identification of most plant species (Barneby & Grimes, submitted). The beetle guilds and chemical traits of the Lecythidaceae are the subject of a separate investigation (Berkov & Tavakilian, in prep.; Berkov et al., in prep.).

III. Materials and Methods

A. COLLECTION OF WOOD SAMPLES

The wood samples were obtained from the same trees used for the rearing experiments (Tavakilian et al., this issue) in the field seasons of 1992 and 1993. No collections for phytochemical studies were made in 1991. After the trees were felled, a sample of 5–10 cm^3 wood was collected consisting mostly of heart wood with small portions of bark. The wood cubes were stored in tightly sealed vials filled with methanol or hexanes. Following transportation to New York, the samples were stored in a freezer at –20°C.

B. EXTRACTION

The wood samples, including the remaining methanol or hexanes, were homogenized in a blender under the addition of 150 ml methanol (Fig. 1). The homogenate was agitated for 1 hr, filtered, and extracted a second time with 100 ml methanol. The two extracts were combined, then evaporated to dryness. Dried extracts were reconstituted in 10 ml methanol and stored at –20°C. The presence of tannins in each sample was determined visually using four categories (abundant, present, trace amounts, absent; see legend to Table I for coding system).

C. PARTIAL PURIFICATION OF EXTRACTS

Five ml of the crude extract were partitioned between 50 ml DCM (dichloromethane) and 25 ml water. The DCM phases were evaporated to dryness, reconstituted in 1 ml methanol/DCM, 2:1, and stored at –20°C until analysis (**DCM-phase** in Fig. 1). The water phases (**water-phase I** in Fig. 1) underwent solid phase extraction on small extraction columns filled with 5 cm^3 presoaked polyamide CC (Scientific Sorbents). The columns were conditioned with 10 ml water using a vacuum manifold, then 4 ml of the water phases were absorbed onto the column while applying vacuum. The columns were eluted with 10 ml water and then with 10 ml methanol. Water and methanol phases were collected separately, evaporated to dryness, and reconstituted in 1 ml of water or methanol, respectively (**water phase II** and **methanol phase** in Fig. 1). They were stored at –20°C until further analysis.

D. ANALYSIS OF DICHLOROMETHANE-PHASE

The DCM-phases were applied onto 20 × 20 cm Silica Gel 60 F-254 plates for TLC-analysis. Plates were developped in DCM/ethyl acetate, 4:1. Chromatograms were evaluated under UV 254 nm, UV 366 nm, and white light. All plates were sprayed with vanillin/sulfuric acid, and a duplicate of each plate with Dragendorff's reagent. In addition, each sample (50 μl of a 1:10 dilution) was analyzed by analytical HPLC using a Nucleosil C-18 column (5 μm, 4.6 × 250 mm) and a photodiode array detector. The samples were separated in a linear gradient from 80% solvent A in B to 100% solvent B in 60 min, continuing at 100% B for 5 min at a flow rate of 1 ml/min. The elutions were detected at 200–400 nm. Solvent A was 2% phosphoric acid in water, and solvent B was acetonitrile.

E. ANALYSIS OF WATER-PHASE II AND METHANOL-PHASE

The water-phase II and methanol-phase of each sample was analyzed by TLC using 20 × 20 cm Silica Gel 60 F–254 plates and *n*-butanol/acetic acid/water, 4:1:1, as mobile phase. The

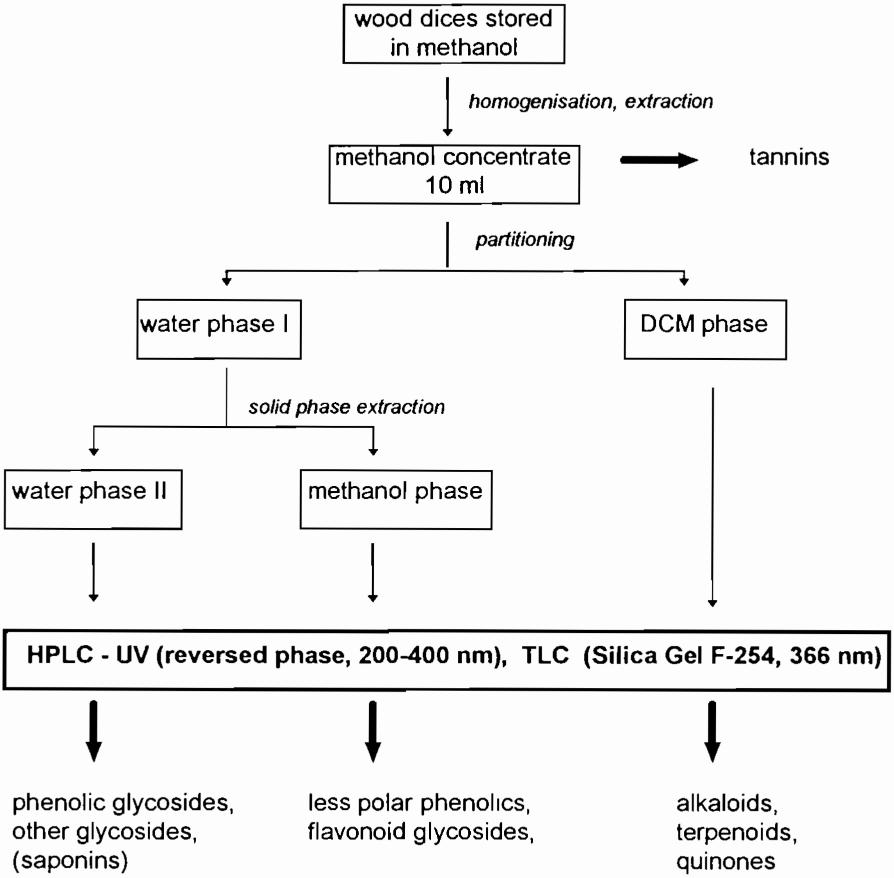


Fig. 1. Extraction scheme for Leguminosae wood samples.

chromatograms were again evaluated under UV-light at 254 nm and 366 nm. Several samples were analyzed repeatedly at different concentrations. In addition, each sample was analyzed by HPLC (50 µl, undiluted in most cases) under the same conditions described above for the DCM-phases. However, the following gradient was applied: linear from 100% A in B to 65% A in B in 60 min, then linear to 100% B in 5 min at a flow rate of 1 ml/min.

IV. Results and Discussion

A. PHYTOCHEMICAL ANALYSIS (TABLE I)

All samples were extracted and partially purified according to the procedure outlined in Figure 1. This separation protocol was necessary because TLC- and HPLC-analysis of the unpurified extract proved to be impossible due to the presence of tannins. The crude extracts, however, were used to visually assess the presence of tannins in a semiquantita-

(Text continues on p. 369)

TABLE I

Chromatographic Analyses of Leguminosae wood samples

Plant taxon/collection[a]	**DCM-phase**	**DCM-phase**	**MeOH-phase**	**MeOH-phase**	**H_2O-phase II**	**H_2O-phase II**	**crude extract**
	TLC Rf/365/Van/Drag[b]	HPLC/UV[c] Rt min (λmax,nm)	TLC Rf/365[b]	HPLC/UV[c] Rt min (λmax,nm)	TLC Rf/365[b]	HPLC/UV[c] Rt min (λmax,nm)	TANNINS[d] (color in white light)
Swartzieae							
Bocoa prouacensis							
L1744	++/bl,gr/2re/ 05	+ (220,320)	9, 95/ye-gr	49 (220,312), 51 (220,290,320)	--	28 (220,280)	+++
L1873[e]	++/bl,gr/1re/ 05	19 (210,300)	.8,.9/bl	--	+/bl	--	+++
M23496	++/bl,gr/2re/--	17 (210-300os)	9/bl	+,58(220,250,280)	--	--	+++
Swartzia panacoco							
L1804	85/gr/--/--	--	--	--	--	16 (220,280)	+
S panacoco var *sagotii*							
M23615	--/--/--/--	+, lc	++/bl	46 (210,325)	--	--	++
S polyphylla							
L1735	+/gr/--/--	--	+/pu,gr	33 (230,290)	+/pu-ye	33 (230,290)	-- (ye)
M23413	++/pu,gr/1re/--	--	+/-	33 (230,290)	+/1ye-gr	32 (230,290)	+
M23594	+/gr/pu/--	--	+/pu,gr	--	++/bl,1wh-ye	33 (230,290)	++
CAESALPINIACEAE							
Cercidieae							
Bauhinia guianensis							
M23471	+/bl,gr/1re/--	4 (260),15 (200)	+/ab-br	+ (200)	++/ab,bl	21 (260)	+++
M23641	+/ab/3re/--	--	+/ab-br	+ (200)	++/ab,bl	20(260),25 (200)	+++
M23678	++/ab,ye/2re/--	4(260),++(200-220)	+/ab	+ (200)	++/bl,pu	20(260),25 (200,260)	+++
Bauhinia outimouta							
M23559	++/ab,bl/ye,gr/--	++,29 (230,340)	+/ab-bl	++ (200)	++/bl,pu	4,26 (230)	+++
M23626[e]	++/ab,bl/ye,br/.1	29,31 (230,340)	++/ab-bl,wh,gr	++ (200)	++/bl,pu	4,26,38 (230)	+++
Cassieae							
Chamaecrista apoucouita							
L1823	++/bl,or/ye/--	+(200), 39(230,300)	.9/gr	45(200), 48(220,330)	--	--	+++

TABLE I contd.

Plant taxon/collection[a]	**DCM-phase**	**DCM-phase**	**MeOH-phase**	**MeOH-phase**	**H_2O-phase II**	**H_2O-phase II**	**crude extract**
	TLC Rf/365/Van/Drag[b]	HPLC/UV[c] Rt min (λmax,nm)	TLC Rf/365[b]	HPLC/UV[c] Rt min (λmax,nm)	TLC Rf/365[b]	HPLC/UV[c] Rt min (λmax,nm)	TANNINS[d] (color in white light)
Dicorynia guianensis							
M23447	+/gr/1or/--	--	+/ab-br	++(200), ++(220,300)	++/wh,ye	25 (220,280)	+++
Caesalpinieae							
Sclerolobium paraense							
M23542	+/bl,gr/pu/--	+	+/bl,ye	30(210,240,280), 45 (240,365)	+/gr-ye	25,33 (220,280)	+++
Sclerolobium sp							
M23567[e]	+/bl,gr/pu/--	+ (200)	+/gr	+ (200)	+/bl,gr,ye	25 (220,280)	+++
Vouacapoua americana							
M23459	+/bl,gr/pu/--	52,53 (220)	.9/ye-wh	47 (220,330)	--	–	+++
M23680	+/gr/pu/.05	52 (220)	9/bl-wh	47 (220,330)	--	–	+++
Detarieae							
Crudia bracteata							
L1733	++/gr,pu/1ye/--	--	++/wh,bl,gr	35 (200,280)	+/bl	+ (220,280)	+++
L1773[e]	++/gr,pu/pu/nd	--	+/ab,ye	35 (200,280)	+/ab	–	+++
L1779	++/gr,pu/1ye/--	--	+/ab	34 (200,280)	++/ab-pu,ye	35 (220,265)	+++
M23492	++/gr,pu/1ye/--	24 (200,280)	+/ab	36 (200,280)	+/pu	–	+++
M23676	++/gr,pu/1ye/--	--	+/ab	34 (200,280)	+/ab	+	+++
Eperua falcata							
M23384	+/gr,pu/pu/nd	19(220,300), 51 (220)	8/gr	37 (210,280), 51 (220,290)	7/ye-or	+	++
E grandiflora							
L1865	2 at 0.5/bl/--/--	+, lc	9/or	++ (200)	.5/pu, .4/br	–	+++
E rubiginosa							
L1851	--	+, 53 (220)	+/ab	26 (215,270), 60 (215,265)	+/ab .9/gr	+	++
Heterostemon sp.							
M23467	+/bl/ye/--	--	.9/ye-gr	29,34(200,280) +	6/bl	++,38(230,290)lc	+++
M23470	--	++ (200) lc	+/--	35,47 (200,280)	.6/ab	–	+++

TABLE I contd

Plant taxon/collection[a]	**DCM-phase**	**DCM-phase**	**MeOH-phase**	**MeOH-phase**	**H_2O-phase II**	**H_2O-phase II**	**crude extract**
	TLC Rf/365/Van/Drag[b]	HPLC/UV[c] Rt min (λmax,nm)	TLC Rf/365[b]	HPLC/UV[c] Rt min (λmax,nm)	TLC Rf/365[b]	HPLC/UV[c] Rt min (λmax,nm)	TANNINS[d] (color in white light)
Peltogyne venosa							
L1686	++/bl,gr/+re/--	9,10(200,230,280) ++	9/ye/day: 2pu[2]	39,40 (200,230,280)	.9/gr	40,41 (200,230,280)	+++ (pu)
M23622	++/bl,gr,or/+re/.05	9,10(200,230,280) ++	9/ye/day: pu[2]	40,41 (200,230,280)	.9/gr	40,41 (200,230,280)	+++ (pu)
M23632	+/bl,gr,ye/+re/nd	8,9 (200,230,280) ++	.9/gr/day pu[2]	40,41 (200,230,280)	--	--	++
Amherstieae							
Macrolobium bifolium							
L1813	+/pu/--/--	++, lc	+/ab,bl	35 (200,280)	+/ab	++ (200,220) lc	++
MIMOSACEAE							
Ingeae							
Abarema barbouriana							
M23659	++/br,pu/ye,pu/ 1 /.5/.7	++ (200) lc	9/ye-gr,bl	+ (230,290), 63 (220)	+/ab	+ (200) lc	+
A. jupunba							
L1875	++/ab.br/pu/--	++ (200) lc	.9/ye-gr	+(230,290) 68,69 (220)	--	--	+
A. jupunba var trapezifolia							
M23688	++/br,bl,gr/ye,pu/--	++ (200) lc	9/ab	69 (220)	+/pu	+ (200) lc	– (ye)
Enterolobium schomburgkii							
L1763	+/ab,pu/pu,gr/n	++ (200)	+/ab	60 (220)	+/ab,ye	+,25(200,260,300) lc	– (ye)
L1874	++/gr,bl,ye/re,ye/n	++(200, >400) lc	.9/ye,bl	69 (220), ++	+/ab,ye-wh	23(220,280) lc	+
M23652	++/ab,bl/br/--	++ (200) lc	9/ye, ab	69 (220)	+/ye,bl	+, 23(220,280) lc	++
Hydrochorea corymbosa							
L1818	+/ab,gr,bl/ye,pu/ 0 5	+, lc	+/ab,gr	+, 41 (200,300) 68, 69 (220)	+/pu	--	++
Inga cf alba							
L1749	--/--/ 5,gr/nd	--	--	--	.7/ab	--	++
Inga sp # 1							
M23456	++/ab,bl,ye/re,or/ 0 5	++ (few >400)	9/ye, +/pu	50,51(240,350) 68,69 (205,215,310)	+/pu,bl	+, lc	+++
M23654	++/ab,pu,br/ye,pu/nd	++ (200, 1> 400)	.9/ye, +/bl	68,69 (os)	--	++, lc	++
Inga sp # 2							
M23669	+/bl,ye/.7,gy/--	++ (200)	+/bl	++ (200)	+/ab	+, lc	++

TABLE I contd.

Plant taxon/collection[a]	DCM-phase	DCM-phase	MeOH-phase	MeOH-phase	H_2O-phase II	H_2O-phase II	crude extract
	TLC Rf/365/Van/Drag[b]	HPLC/UV[c] Rt min (λmax,nm)	TLC Rf/365[b]	HPLC/UV[c] Rt min (λmax,nm)	TLC Rf/365[b]	HPLC/UV[c] Rt min (λmax,nm)	TANNINS[d] (color in white light)
Inga sp. # 3							
M23549	++/ab,ye,or/re,gy/--	+ (1>400)	9/ye +/bl	++ (200), 68,69 (220,310)	4/bl	27 (220 290) lc	+++
Inga sp. # 4							
M23491	05/ye/re,pu,gy/ 05	+, lc	+/gr	++ (200)	.3/ab	--	+++
M23501	+/ab,or/br,re/.05	73 (230) lc	9/ye +/bl	++ (200) 68,69 (220,310)	--	+, lc	+++
M23660[e]	+/br,pu/ 7,gy/--	+, lc	9/ab .6/bl	++ (200) 68, 69 (220,310)	--	++, lc	+++
Inga sp indet							
L1861[e]	+/br/gy/--	+, 17 (220,275)	9/gr, 6/day:re	--	+/ab	+, lc	+
L1864	++/ab,bl/or,br/ 05	++ (few >400)	.9/ye, .6/day:re	+ (210,290)	+/ab	+, lc	+++
L1871	++/ab,bl,ye/or,br/.05	++ (few >400)	9/ye	+, 50,51(240,350)	--	+, lc	++
Zygia racemosa							
M23670	+/ab,gr/pu,gy/--	+, lc	+/ab	++ (200) lc	+/ye,bl,pu	+ (200) lc	+
M23686	++/ab,ye,gr/pu,gy/--	+, lc	--	++ (200) lc	+/bl,pu	+ (200,280) lc	-- (ye)
Zygia sabatieri							
L1747	++/bl,pu,ye/1re,br/--						
M23397[e]	+/br,pu/ye,gy/ 05	+, lc	+/ye,wh,bl	++ (200,280)	--	++ (200,280) lc	++
M23468[e]	++/ab,or,bl/pu,re/ 05	++ (200, few >400)	--	38 (210,240,280,330) 45 (250,365)	+/ab	n	++
M23605	++/ab,ye/br,pu/--	++ (200) lc	+/ab 6/day re	++ (200,280)	+/bl,pu,gr	++,lc	-- (ye)
Zygia tetragona							
L1752	++/bl,or/br/.05/ 7	+,lc	+/ab,pu	++(200,230,280)	+/ab	--	+++
Zygia cf tetragona							
M23638	++/ab/gy/nd	+,lc	+/ab,bl	++ (200,230,280)	+/ab,wh	27(220,280) lc	++
Parkieae							
Parkia velutina							
L1770	+/ab,gr/1re,pu/--	+,lc	--	+,lc	--	--	grey

TABLE I contd

Plant taxon/collection^{a}	DCM-phase	DCM-phase	MeOH-phase	MeOH-phase	H_2O-phase II	H_2O-phase II	crude extract
	TLC Rf/365/Van/Drag^{b}	HPLC/UV^{c} Rt min (λmax,nm)	TLC Rf/365^{b}	HPLC/UV^{c} Rt min (λmax,nm)	TLC Rf/365^{b}	HPLC/UV^{c} Rt min (λmax,nm)	TANNINS^{d} (color in white light)
Mimosieae							
Pseudopiptadenia suaveolens							
L1743	++/gr.bl/re,pu/ 05	+,lc	+/bl,or	++ (200,280, 1>400)	++/ye,gr,pu	++, lc	++
M23575	++/gr,bl/bl.pu/nd	20 (220,290,320)	+/br,ye	++ (200)	+/br,pu	+, 24 (220,280)	+++
FABACEAE							
Dalbergieae							
Andira coriacea							
M23646	++/gr,bl/re,or/ 05/ 14/ 43/ 6/ 71/ 81	++/20,23,28,29, 32 (os)	++/ye,ab	++,55(260)	++/ye,bl	+, 32, 35 (220,280,320)	+++
Hymenolobium petraeum							
M23694	++/bl,gr/re/ 04/ 07/ 11/ 2/ 36/ 45/ 67/ 79	++/20,23,24,28, 29,31,34 (os)	++/bl,gr,wh	--	++/bl,gr,ye	+ (220,290,330)	+++
Machaerium sp.							
L1815	++/bl,gr/pu,re/--	32(230,295,340)lc	+/ab	--	+/gr	+, lc	+++
Paramachaerium ormosioides							
L1870	++/ab/gy,1re/--	++, lc	--	--	--	--	+++
Sophoreae							
Acosmium nitens							
M23644	++/gr,pu,or/re,ye / 67	++, 28 (os)	+/or bl,ab	56,57 (200,270,300,350)	+/or	56,57 (210,270,300,350)	+++
Diplotropis purpurea							
L1712	+/ab.bl/n/.01	++,19,20,23,26, 28,29,34 (os)	+/gr,br	38,44,47 (215,270,335)	+	+, 15 (205)	+
Dussia discolor							
M23412	++/ab,ye,or/or,pu,bl/n	++,19,27,28,31,33,41 (os)	+/pu,ab	47 (220, 290) 56 (260)	+/bl,pu	--	-- (ye)
M23625	++/ab,bl/re,gy/ .00/.08/.15	+,18 (200)	+/gr	+ (230,290)	+/ab	--	++
Monopteryx inpae							
L1739	++/gr,bl,or/re,ye/ 29/ 44/ 5/ 62/ 83/ 98	++, 21,23 (os)	++/bl,wh	+, 72 (230)	++/bl,ye,wh	32 (200,230,290)	+++

TABLE I contd.

Plant taxon/collection[a]	**DCM-phase**	**DCM-phase**	**MeOH-phase**	**MeOH-phase**	**H_2O-phase II**	**H_2O-phase II**	**crude extract**
	TLC Rf/365/Van/Drag[b]	HPLC/UV[c] Rt min (λmax,nm)	TLC Rf/365[b]	HPLC/UV[c] Rt min (λmax,nm)	TLC Rf/365[b]	HPLC/UV[c] Rt min (λmax,nm)	TANNINS[d] (color in white light)
Ormosia nobilis							
M23548	++/gr,bl,or/re,gy/ 10/ 29/ 52/ 61/ 86	26 (220,290,330)	+/bl	--	--	--	++
M23611	++/gr,bl/ye,or/ 11/ 31/ 55/ 64/ 85	++,20,29,32,35, 37 (os)	9/day.re +/bl	--	--	--	+
Ormosia paraensis							
L1796	++/gr,bl,ye/re,or/ .05/ 15/.3/.5/.8	26,32 (os) ++	9/re,bl,gr/day re	45,53 (200,230,280)	+/ye,gr,wh/day re	34,35 (200,230,280)	+++
Dipteryxeae							
Dipteryx sp.							
L1797	+/bl,gr/br/nd	+, 15(200,265) 26 (265,320)	+/ye,bl,pu	51,52 (270,330)	+/ab	–	n
Taralea oppositifolia							
L1848	++/bl,or/re,ye/.18,gr?	++, 18, 19 (os)	++,bl,wh	--	++/bl,pu	+,31(210,290,340)	– (ye)
Tephrosieae							
Lonchocarpus sp							
L1838	+/pu,or/re,gy/nd	++, 59,60(200,230)	+/gr	+, 57 (260)	+/ab	–	+
Poecilanthe hostmannii							
M23668	++/gr/pu,2re/ --	--		+, 45(220,265,340)		+, 29(220,270)	– (ye)
Phaseoleae							
Dioclea macrocarpa							
M23556[e]	++/ab,gr/pu,bl/ --	--	--	–	+/ab	--	– (ye)

Table 1 footnotes:

[a] Authors of all plant names, and notes pertinent to the collection and determination of these plants, are listed in Tavakilian et al., this issue. Specimens examined are identified by their collection number, preceded by a letter indicating the collector: L, Denis Loubry; M, Scott Mori. The specimens were identified by J. Grimes.

[b] The following characteristics are listed for TLC-analysis: Rf-value/fluorescence under 365 nm UV-light/color after treatment with Vanillin-Spray/color after treatment with Dragendorff Spray; Rf-values are given only when 1 or 2 major compounds were distinguishable; if more compounds were detected, the following symbols were used: +, to 5 major compounds; ++, more than 5 compounds; —, tested, but nothing detected; nd, no data available All plates were observed at 365 nm UV-light and then treated with NH_4OH vapors; color changes were observed, which are indicated by a hyphen between color codings. Example: .9/bl-gr means: the compound with Rf .9 was blue at UV-365 and changed to green after NH_4OH treatment. TLC plates of DCM phases were sprayed with Vanillin-H_2SO_4 (= Van). Dragendorff positive bands are indicated with their Rf value. Color descriptions: ab, absorbing (dark, quenching fluorescence at 254 nm); bl, blue; br, brown; gr, green; gy, grey; or, orange; pu, purple; re, red; wh, white; ye, yellow; day, visible in white light (daylight). See Material and Methods for the different solvent systems used.

[c] The following characteristics are listed for HPLC-analysis: Retention time (min), and the UV absorption maxima (λ_{max}) of the compound detected via photodiode array detection (200–400 nm). The following symbols were used to indicate the presence of complex compound patterns: +, to 5 major compounds; ++, more than 5 compounds; lc, low concentration indicated by low absorbance (below 0.1 AUs); os, off scale; —, tested, but nothing detected; nd, no data available. See Material and Methods for the different gradients used.

[d] The color of the crude extract was used to judge the abundance of tannins: +++, dark brown indicating abundance; ++, sienna and mid-brown indicating presence of tannins; +, tan, tannins present but not dominant; —, tannins not visible, color of extracts is given in parenthesis, color codings as in TLC-analysis; nd, no data available.

[e] These collections are not listed in Tavakilian et al., this issue, because they did not yield any cerambycid emergences. They were analyzed for their chemical patterns to obtain additional support for the results.

tive manner using four different categories (see Table I). The partitioning into DCM and water-phase provided initial separation of polar and nonpolar compounds, and the subsequent solid-phase extraction of the water-phase allowed for the removal of tannins. This separation into the three phases was highly reproducible, and results obtained from extractions of the same tree species were nearly identical. Cross contamination of phases was tested by HPLC using DCM-phases with MeOH-gradient conditions and vice versa, and was found to be negligible—e.g., major substances of the MeOH-phase were rarely seen in the DCM-phase or the H_2O II-phase. Only in a few cases, when concentrations of a particular metabolite were exceptionally high, was cross contamination noted; e.g., the purple peltogynol in *Peltogyne venosa* was present in all phases but mostly accumulated in the MeOH-phase. Therefore, the chromatographic analysis of each of the three phases obtained from each sample yielded a distinctive phytochemical pattern. The evaluation of the TLC-analysis allowed the detection of absorbing compounds as well as substances with poor absorption characteristics, such as terpenoids. The HPLC-analysis (conducted with a photodiode array detector) yielded primarily results on the occurrence of optically active substances. Some compounds were tentatively identified by comparison with data available in the literature, but generally no attempt was made to conduct structural elucidations of the constituents.

Table I summarizes the results of the chromatographic analyses (TLC, HPLC) from all three phases of each extract using a consistent coding system. The legend to Table I specifies the codes used and includes an example for decoding the information. Retention times and Rf-values are given for dominant constituents, as are their absorption and fluorescence characteristics. Although structural elucidations were not conducted, this procedure allowed for the description of phytochemical patterns in each sample.

B. TAXONOMY OF LEGUMINOSAE HOST PLANTS

A total of 80 legume wood samples belonging to 51 taxa in 33 genera of three families and one tribe *incertae sedis* (Swartzieae) were subjected to chromatographic analysis and evaluation of their beetle guilds. In accordance with Cronquist (1981) and with the taxonomic arrangement used in Tavakilian et al. (1997), we recognize the Leguminosae at the ordinal level (Fabales, in Cronquist, 1981), and are using family-level distinctions for the Mimosaceae, Caesalpiniaceae, and Fabaceae. Tribes within these families are recognized according to Polhill and Raven (1981). The plant taxa are listed in taxonomic arrangement in Tables I and II according to Polhill and Raven (1981), with a few modifications in the Mimosaceae according to Barneby and Grimes (1996, 1997).

Members of the Leguminosae are usually recognized by their leguminous fruits. The group is commonly divided into three families (sometimes considered subfamilies): The Mimosaceae are characterized by regular flowers; the Caesalpiniaceae usually have regular to irregular flowers in which the lateral petals are internal to the abaxial petals prior to anthesis, and erect embryonic seeds; the Fabaceae have irregular flowers in which the lateral petals are external to the abaxial ones, and they possess curved embryonic seeds. The tribe Swartzieae is placed in either the Fabaceae or the Caesalpiniaceae (Polhill & Raven, 1981) and is not included in any of the three Leguminosae families in this paper due to its uncertain taxonomic status. Affinities are seen to some tribes of the Caesalpiniaceae, and the basal groups of the Fabaceae, Sophoreae, and Dalbergieae (Polhill & Raven, 1981). Species of Leguminosae are dominant members of most ecosystems in the world including the lowland neotropical rain forest found in the Sinnamary River Basin, where they constitute the most dominant plant family. With 51 sufficiently identified taxa, the Leguminosae were the largest taxonomic group of host plants represented in the Sinnamary study. A total of 85 samples were analyzed during the field seasons of 1992 and 1993, and 80 are included in Table I. Several samples were omitted because botanical identication of the samples below the family level was impossible. The genus *Inga* (Mimosaceae) is currently under revision (Poncy, in prep.), and identifications were not available for the majority of samples. As this did not affect the interpretation of our results, all *Inga* specimens are included in the evaluation.

C. CERAMBYCIDAE

A brief synopsis of the biology of the Cerambycidae, also called longicorns, long-horned beetles, or timber beetles, is presented in Hequet & Tavakilian, 1996). A total of 92 cerambycid taxa were found on the 85 trunks of Leguminosae in the course of three field seasons (1992–1993) in the Sinnamary River Basin. Most taxa are listed and referenced under their host plant in Table I in Tavakilian et al. (this issue). Undescribed species are listed under their current working numbers and are included in the total count of taxa. These 92 beetle species emerged from one to several host plants.

Figure 1 in Tavakilian et al. (this issue) provides a preliminary analysis of the feeding and reproductive strategies of the longicorn species found on leguminous host plants. It appears that exactly one-half of the beetle species were found on only one plant sample. Often these beetles are also documented only by a single emerging individual. We decided that more data need to be gathered before any judgment on their reproductive strategy can be made. They may be rare specialists, but other demographic or climatic factors may play a role in their distributional patterns. It certainly seems premature to label them "monophagous," because a continuation of the study may reveal other host plants. The rare emergences could just reflect a low survival rate of the larvae that may not have grown up in their optimal host plant. No further assumptions about the host specificity of these species are therefore made in the present study.

Most cerambycid species emerged from 2–5 legume host plants. They were considered oligophagous. With only a few exceptions, the host plants of the oligophagous beetles are taxonomically related. Seven beetle species emerged from 6–11 legume host plants. These were found in all three subfamilies of the Leguminosae, but some also in other plant families (see Tavakilian et al., this issue). The latter are definitely generalist with no particular preference to legume host plants, e.g., the longicorn species *Nyssodrysternum signiferum*, *Mecometopus globicollis*, and *Toroneus perforator*.

The cerambycid taxa found on the Leguminosae belong to many tribes (see Tavakilian et al., this issue). For example, the taxa included in Table II belong to eight different tribes. The implications of this finding are discussed below.

D. PHYTOCHEMICAL PATTERNS AND PATTERNS OF HOST SPECIFICITY (TABLES II AND III)

Table II represents a summary of the chemical analyses on the Leguminosae wood samples, relevant chemical information compiled from literature searches, and a synopsis of the cerambycid beetle emergences. This information is shown for each taxon as listed in Table I, but individual collections are not distinguished. The taxonomic arrangement of the taxa was maintained and is discussed below in reference to chemical data and cerambycid emergences. Tavakilian et al. (this issue) present additional data on legume host plants from plant collec-

(Text continues on p. 381)

TABLE II

Chemical patterns and longicorn guilds of Leguminosae in the Sinnamary River Basin

Plant taxon	**Summary chemical profile** (from TABLE I)	**Other compounds reported** (wood and bark only)	**Cerambycid guilds**[b]	**Cerambycid frequencies**[c] 91/92/93
Swartzieae				
Bocoa prouacensis	abundance of non-polar, vanillin-positive and UV-positive compounds indicating aromatic compounds; one specimen with dominant polar phenylpropanoids.	ILDIS[a] - no entry	*Cycnidolon approximatum* *Odontocera molorchoides*	01/01/-- 08/05/03
Swartzia panacoco	one polar, aromatic compound with Rt = 16 (λ_{max}=220,280)	ILDIS - no entry other species: coumarins and other benzopyranoids, isoflavonoids, saponins	*Agaone notabilis* *Odontocera molorchoides* *Oedopeza ocellator*	--/07/-- --/14/-- --/04/--
S panacoco var *sagotii*	one dominant phenylpropanoid in MeOH-phase with Rt=46 (λ_{max} =230,325)	ILDIS - no entry	*Agaone notabilis* *Odontocera molorchoides* *Odontocera* sp. nov. 1018	--/--/03 --/--/02 --/--/04
S polyphylla	many non-polar, vanillin-positive, but UV-negative compounds indicating the presence of terpenoids; one dominant, polar, aromatic compound with Rt=32 (λ_{max} =230,290);	ILDIS - no entry isoflavone (Dubois & Sneden, 1992)	*Agaone notabilis* *Colobothea hirtipes* *Cycnidolon approximatum* *Odontocera molorchoides* *Odontocera* sp. nov 1018	--/--/01 --/--/01 --/--/10 --/--/08 --/01/17
CAESALPINIACEAE				
Cercideae				
Bauhinia guianensis	simple, polar and non-polar, aromatic compounds; abundance of vanillin-positive and UV-negative compounds indicates the presence of aliphatic or terpenoid compounds	ILDIS: saturated, un-branched alcohols and their ferulic and *p*-coumaric acid esters (Achenbach et al., 1986, FIGURE 2), chalcones	*Acanthocinini* sp nov 951 *Colobothea* sp nov. 322 *Estola* sp. nov 435 *Hilobothea latevittata* *Lissonotus equestris* many unicates	--/--/21 --/--/06 --/--/11 --/--/98 --/--/07

TABLE II contd

Plant taxon	**Summary chemical profile** (from TABLE I)	**Other compounds reported** (wood and bark only)	**Cerambycid guilds**[b]	**Cerambycid frequencies**[c] 91/92/93
Bauhinia outimouta	non-polar flavonoids and other non-polar, aromatic compounds; polar, simple, aromatic compounds	ILDIS - no entry **other species**: see *B. guianensis*	*Colobothea* sp. nov. 322 *Hilobothea latevittata* *Estola* sp. nov. 435 (see Tavakilian et al , 1998)	--/--/11 --/--/24 --/04/--
Cassieae				
Chamaecrista apoucouita	abundance of non-polar, aromatic compounds (anthraquinones?), and other vanillin-positive compounds (terpenoids?), polar compounds absent	ILDIS - no entry **other species** anthraquinones and imidazole alkaloids in whole plants	*Odontocera* sp. nov. 1018	--/XX/--
Dicorynia guianensis	non-polar, vanillin-positive, but UV-negative compounds present (terpenoids, aliphatics), abundance of polar, aromatic compounds with one dominant at Rt=25 (λ_{max} =220,280), similar to *Sclerolobium*	ILDIS· tryptamine	generalists	
Caesalpinieae				
Sclerolobium	non-polar, vanillin-positive, but UV-negative compounds present; polar, aromatic compound with Rt=25 (λ_{max} =220,280), similar to *Dicorynia*	ILDIS - no entry	many unicates 3 *Chrysoprasis* species (Tavakilian et al , 1998)	
Vouacapoua americana	two dominant, non-polar compounds with Rt=52 (λ_{max} =220) could correspond to vouacapane diterpenoids, one phenylpropanoid present with Rt=47 (λ_{max} =220,330)	ILDIS, Hegnauer, 1994. piceatannol, methyl vouacapenoate (cassane and vouacapane diterpenoids)	unicates	
Detarieae				
Crudia bracteata	abundance of non-polar, vanillin-positive compounds indicating the presence of terpenoids; one dominant aromatic compound with Rt=35 (λ_{max} =200,280) in MeOH-phase, see *Macrolobium*	ILDIS - no entry **other species** apigenin in *C. amazonica* (Hegnauer, 1994)	*Cicatrizocera bilistrata* *Cosmotoma adjuncta* *Macronemus antennator* *Odontocera* sp. nov. 1018 one unicate	12/00/08 01/--/-- --/--/01 02/--/--

TABLE II contd

Plant taxon	**Summary chemical profile** (from TABLE I)	**Other compounds reported** (wood and bark only)	**Cerambycid guilds**[b]	**Cerambycid frequencies**[c] 91/92/93
Eperua falcata	non-polar subtances at Rt=19,51, see *Vouacapoua*, polar phenolic compounds in MeOH-phase at Rt = 37, 51	ILDIS: oleyl alcohol, eperuic acid (wood resin, labdane diterpenoid)	*Brasilianus plicatus*	--/XX/XX
			Chlorida curta	--/--/01
			Cycnidolon batesianum	--/--/01
			Polyrhaphis spinosa	--/01/--
			Pseudaethomerus lacordairei	--/01/03
			Sphaerion cassum	--/--/01
E. grandiflora	abundance of compounds in MeOH-phase with λ_{max} =200 (terpenoid gylcosides, saponins?)	ILDIS - no entry **other species**: see *E. falcata*	*Brasilianus plicatus*	XX/XX/--
			Sphaerion cassum	XX/XX/--
			generalists	
E rubiginosa	non-polar compounds, similar to *Vouacapoua*, phenolics in MeOH-phase present	ILDIS - no entry **other species**: see *E. falcata*	*Brasilianus plicatus*	XX/XX/XX
			Chlorida curta	--/01/--
			Cycnidolon batesianum	01/--/--
			Macronemus antennator	01/--/--
			Polyrhaphis spinosa	01/--/--
			Pseudaethomerus lacordairei	01/--/01
			Sphaerion cassum	05/--/--
Heterostemon sp.	few non-polar compounds, two dominant, aromatic compounds in MeOH-phase with λ_{max}= 200,280, see also *Crudia* and *Macroblobium*	ILDIS - no entry	*Lissonotus equestris*	--/--/02
			Pseudaethomerus lacordairei	--/--/02
Peltogyne venosa	purple flavonoids present in all fractions; other non-polar, vanillin-positive, and UV-positive compounds (anthraquinones?)	ILDIS - flavonoids (butin, liquiritigenin, mopanol, peltogynol, pubeschin, and others)	*Brasilianus plicatus*	--/--/01
			Sphaerion cassum	--/01/--
			generalists	
Amherstieae				
Macrolobium bifolium	few non-polar compounds; one dominant, aromatic compound in MeOH-phase with Rt=35 (λ_{max} =200,280), see *Crudia* and *Heterostemon*	ILDIS - benzofuranoids, benzopyranoids, steroids	*Cosmotoma adjuncta*	01/--/--
			Macronemus antennator	01/--/--
			Pseudaethomerus lacordairei	--/--/02

TABLE II contd

Plant taxon	**Summary chemical profile** (from TABLE I)	**Other compounds reported** (wood and bark only)	**Cerambycid guilds**[b]	**Cerambycid frequencies**[c] 91/92/93
MIMOSACEAE				
Ingeae				
Abarema barbouriana	abundance of non-polar, vanillin-positive, and UV-negative compounds indicating the presence of terpenoids; dominant simple aromatic compounds in MeOH-phase at Rt = 63 to 69 (λ_{max} =220); tannins absent	ILDIS - no entry under *Abarema* or *Pithecellobium*; **other species of** *P* · steroids, saponins (Hegnauer, 1994)	*Hemilissa catapotia* *Thoracibidion ruficaudatum*	--/--/02 --/--/01
A jupunba	as *A barbouriana*	as *A barbouriana*	no emergences, but in Tavakilian et al (1998): *Thoracibidion ruficaudatum* *T. striatocolle*	
A jupunba var trapezifolia	as *A barbouriana*	as *A barbouriana*	*Oedopeza ocellator*	--/--/03
Enterolobium schomburgkii	as *A barbouriana*, but additionally polar, aromatic compound at Rt=23 (λ_{max} =220,280), also weak in tannins	ILDIS - no entry **other species** *E cyclocarpum* (plant part not specified): betulinic acid, 3β-hydroxycoriaceolide	*Oedopeza apicale* *O. ocellator* *Thoracibidion ruficaudatum* *T. striatocolle* several unicates	01/--/-- --/05/-- --/06/-- --/06/--
Hydrochorea corymbosa	non-polar and UV-positive compounds, some vanillin-positive, aromatic compounds in MeOH-phase with Rt = 69 (lmax=220); very polar compounds almost absent, similar to *Abarema*	ILDIS - no entry	*Oedopeza apicale* *O. ocellator* *O. setigera* *Thoracibidion ruficaudatum* *T. striatocolle* generalists	23/--/-- 56/--/-- 06/--/-- 04/--/-- 93/--/--
Inga (entire genus)	abundance of non-polar compounds, vanillin-positive with λ_{max} <200; occassionally vanillin-red substances correlating to compounds with λ_{max} >400; these also erratically in *Enterolobium* and *Zygia*; frequently Dragendorff-positive substances with low Rf-values (pipecolic acids?), simple aromatic compound in MeOH-phase with Rt=69 (λ_{max} =220), as in most other Ingeae; very polar compounds almost absent	ILDIS mostly seeds investigated (pipecolic acid derivatives and albizziine); wood: *I. punctata:* betulinic acid, lupeol (lupane triterpenoid), saponins in some species (Hegnauer, 1994)	*Hemilissa catapotia* *Oedopeza apicale* *Oedopeza ocellator* *Chrysoprasis moerens* several unicates	--/--/05 13/--/-- --/02/11 --/--/10

TABLE II contd.

Plant taxon	**Summary chemical profile** (from TABLE I)	**Other compounds reported** (wood and bark only)	**Cerambycid guilds**[b]	**Cerambycid frequencies**[c] 91/92/93
Zygia racemosa	abundance of vanillin-positive, but UV-negative compounds indicating terpenoids or other aliphatic compounds; these include Dragendorff-positive compounds with low Rf-values (pipecolic acid derivatives or albizziine?); polar, simple, aromatic compounds with λ_{max} =200 or λ_{max} =200,280, dominant aromatic compound from other Mimosaceae at Rt=69 is absent, consistently weak in tannin content	ILDIS no entry under *Zygia* or *Pithecellobium*, **other species**· as *Abarema barbouriana* steroids	*Thoracibidion ruficaudatum*	--/--/01
Z sabatieri	as *Z. racemosa*, one specimen with a flavonoid	ILDIS - see *Z. racemosa*	one unicate	
Z tetragona	as *Z. racemosa*, but polar aromatic compounds only in MeOH-phase	ILDIS - see *Z. racemosa*	*Thoracibidion ruficaudatum* *Moacronemus antennator* one unicate	--/09/-- --/XX/--
Z cf tetragona	as *Z. racemosa*	ILDIS - see *Z. racemosa*	no emergences	
Parkieae				
Parkia velutina	non-polar, vanillin-positive, but UV-negative compounds indicating the presence of terpenoids or other aliphatic substances	ILDIS - no entry **other species** seeds: pipecolic acid; *P. nitida*· stem exudates, gum (Hegnauer, 1994)	*Polyrhaphis spinosa* In *Parkia nitida* (Tavakilian et al., 1998): *Polyrhaphis spinosa* *Thoracibidion striatocolle*	02/--/--
Mimosieae				
Pseudopiptadenia suaveolens	non-polar, vanillin-positive, but UV-negative compounds indicating the presence of terpenoids; polar, simple, aromatic compounds present	ILDIS - no entry **other species** seeds: pipecolic acid	*Cosmotoma adjuncta* *Thoracibidion ruficaudatum*	--/XX/XX --/05/--

TABLE II contd.

Plant taxon	**Summary chemical profile** (from TABLE I)	**Other compounds reported** (wood and bark only)	**Cerambycid guilds**[b]	**Cerambycid frequencies**[c] 91/92/93
FABACEAE				
Dalbergieae				
Andira coriacea	abundance of non-polar, vanillin-positive and UV-positive compounds, including Dragendorff-positive bands, and possibly anthraquinones, polar aromatic compounds present; many compounds similar to *Hymenolobium;* presence of alkaloids was not confirmed by GC-MS (Greinwald & Meurer-Grimes, unpublished)	ILDIS - no entry **other species**. isoflavonoids, steroids, vanillin, n-methyl-tyrosine; no anthraquinones found acc. to Hegnauer (1994)	*Acyphoderes abdominalis* *Lissonotus equestris* generalists	--/--/01 --/XX/--
Hymenolobium petraeum	abundance of non-polar, vanillin-positive and UV-positive compounds, including at least 6 Dragendorff-positive bands and possibly anthraquinones; polar aromatic compounds also present, many similarities to *Andira*; presence of alkaloids was not confirmed by GC-MS (Greinwald & Meurer-Grimes, unpublished)	ILDIS - no entry	*Acyphoderes abdominalis* listing for *Hymenolobium flavum* (Tavakilian et al., 1998)	--/--/01 13/--/--
Machaerium sp.	abundance of non-polar, vanillin-positive compounds; only one non-polar aromatic compound with Rt=32 (λ_{max} =230,295, 340); polar compounds few; alkaloids absent	ILDIS **other species**: isoflavonoids, simple aromatic compounds, triterpenoids (sap wood), benzopyranoids including coumarins (Hegnauer, 1994)	*Colobothea hirtipes* *Oedopeza ocellator* unicates	--/04/-- --/02/--
Paramachaerium ormosioides	abundance of non-polar, vanillin-positive and UV-negative compounds; very few polar compounds; alkaloids absent	ILDIS - no entry	*Colobothea hirtipes* generalists	19/02/--

TABLE II contd

Plant taxon	Summary chemical profile (from TABLE I)	Other compounds reported (wood and bark only)	Cerambycid guilds[b]	Cerambycid frequencies[c] 91/92/93
Sophoreae				
Acosmium nitens	abundance of non-polar, vanillin-positive and UV-positive compounds; one polar aromatic compound at Rt=56,57 (λ_{max} =200,270,300,350); some non-polar compounds shared with *Hymenolobium* and *Andira*, one Dragendorff positive band, but the presence of alkaloids was not detected with GC-MS (Greinwald & Meurer-Grimes, unpublished)	ILDIS - no entry **other species**: lupeol, sweetinine and other quinolizidine alkaloids	*Acyphoderes abdominalis* *Colobothea hirtipes* *Oedopeza apicale* generalists	--/--/48 --/--/03 --/--/01
Diplotropis purpurea	non-polar and polar, UV-active compounds probably phenolics; weak in tannins, one Dragendorff-positive band in DCM-phase	ILDIS - isoflavonoids, lupeol and steroids; **other species**: quinolizidine alkaloids in *D. martiusii.*	one unicate	
Dussia discolor	abundance of non-polar, vanillin-positive and UV-positive compounds, including alkaloids; polar, simple aromatic compounds present; tannins absent	ILDIS - no entry	one unicate generalists	
Monopteryx inpae	abundance of non-polar, vanillin-positive and UV-positive compounds including at least 6 Dragendorff positive bands, some similar to *Ormosia*; polar, aromatic compounds with one dominant at Rt=32 (λ_{max} =200,230,290)	ILDIS - no entry, essential oils (elemerin) (Hegnauer, 1994)	*Odontocera simplex* generalists	--/05/--
Ormosia nobilis	abundance of non-polar, vanillin-positive and UV-positive compounds, including 5 Dragendorff positive bands; almost no polar compounds found	ILDIS - no entry **other species**: quinolizidine alkaloids (Ricker et al , 1995), triterpenoids (lupeol), benzofuranoids, steroids	generalists few unicates	
O paraensis	abundance of fluorescent, non-polar compounds, red with Vanillin-spray, additional presence of polar, aromatic compounds, five Dragendorff-positive bands in DCM-phase	as *O nobilis*	*Chlorida curta* *Cycnidolon batesianum*	--/01/-- --/01/--

TABLE II contd.

Plant taxon	**Summary chemical profile** (from TABLE I)	**Other compounds reported** (wood and bark only)	**Cerambycid guilds**[b]	**Cerambycid frequencies**[c] 91/92/93
Dipteryxeae				
Dipteryx sp	several non-polar and polar, UV-active compounds, probably phenolics (phenylpropanoids)	ILDIS, Hegnauer (1994): **other species**. *D odorata* benzopyranoids, triterpenoids (betulin, lupenone, lupeol in bark), isoflavonoids, coumarins in entire genus	*Odontocera simplex* *Odontocera* sp nov 392	--/26/-- --/06/--
Taralea oppositifolia	abundance of non-polar, vanillin-positive and UV-positive compounds, one at Rt=18,19, polar compounds also present, *e g* Rt=31 (λ_{max} =210,290,340); tannins absent	ILDIS - no entry, coumarins in entire genus (Hegnauer, 1994)	*Odontocera simplex* *Odontocera* sp. nov. 392 *Oedopeza ocellator*	04/--/-- 55/111/-- 03/--/--
Tephrosieae				
Lonchocarpus sp	non-polar, UV-active and Vanillin-positive compounds, one band is Dragendorff-positive; a few polar phenolics, weak in tannins	ILDIS - seeds investigated for amino acids and alkaloids; **other species** rotenoid and other unusual flavonoids (castilline A-E, longistyline A-C, lonchocarpin), stilbenes, lupenone, lupeol	unicates generalists	
Poecilanthe hostmannii	abundance of non-polar, vanillin-positive, but UV-negative compounds (terpenoids or other aliphatics), polar, aromatic compounds present including a flavonoid at Rt=45 (λ_{max} =220,265,340); no Dragendorff positive bands	ILDIS - no entry **other species** isoflavones, nerolidol (monoterpene)	*Odontocera colon*	--/--/02
Phaseoleae				
Dioclea macrocarpa	Abundance of non-polar, vanillin-positive, but UV-negative compounds indicating terpenoids or other aliphatics; almost no polar compounds present; no Dragendorff positive bands	ILDIS physostigmine from seeds	no emergences	

Table II footnotes:

[a] ILDIS, International Legume Database and Information Service; Bisby et al., 1994, see Literature Cited.

[b] Cerambycid guilds as observed in the samples that were available for chemical analysis. Additional data are provided in Tavakilian et al., this issue, and discussed in the text. Classification of Cerambycidae can be found in Tavakilian et al., this issue. Taxa that did not yield any emergences are not included in Table I in Tavakilian et al., this issue, but were analyzed for their chemical profiles for supporting evidence and are included in Table II.

[c] Cerambycid frequencies are given as cumulative numbers; e.g., emergences from all collections made of one species from 1991 to 1993 were added. —, no collection was made; XX, emergences observed, but an accurate count was not available. Counts from the 1991 field season are included.

TABLE III

Guilds of Cerambycidae on Leguminosae Host Taxa

	Swartzieae	*Bauhinia*	Cassieae/ Caesalpinieae	Detarieae/ Amherstieae	Mimosaceae	*Andira/Hymenolobium/ Acosmium*	*Machaerium/ Paramachaerium*	Dipteryxeae	Other Fabaceae
Cycnidolon approximatum	X								
Odontocera molorchoides	X								
Agaone notabilis	X								
Oedopeza ocellator	⊗				⊗		⊗	⊗	
Odontocera sp nov 1018	⊗		⊗						
Colobothea hirtipes	⊗					⊗	⊗		
Acanthocinini sp nov 951		X							
Colobothea sp nov 322		X							
Estola sp nov. 435		X							
Hilobothea latevittata		X							
Lissonotus equestris		⊗				⊗			
Cicatrizocera bilistrata				X					
Cosmotoma adjuncta				X					
Macronemus antennator				⊗	⊗				
Brasilianus plicatus				X					
Chlorida curta				⊗					⊗
Cycnidolon batesianum				⊗					⊗
Polyrhaphis spinosa				⊗	⊗				
Pseudaethomerus lacordairei				X					
Sphaerion cassum				X					
Hemilissa catapotia					X				
Thoracibidion ruficaudatum					X				
Thoracibidion striatocolle					X				
Oedopeza apicale					⊗	⊗			
Oedopeza setigera					X				
Chrysoprasis moerens					X				
Acyphoderes abdominalis						X			
Odontocera simplex								⊗	⊗
Odontocera sp nov 392								X	

X, cerambycid emergence recorded; ⊗, disjunct distribution tions obtained during the field season of 1991, from other sites in French Guiana, and from the literature. These other samples were not available for phytochemical studies, and were studied only for beetle emergences. Ample supporting evidence can be derived from these data, and they are therefore included in the discussions below, though not listed in Tables II and III. In the second column of Table II, a brief summary of the chemical profiles is given for each plant taxon along with a summary of data available from the literature. The two final columns show a summary of beetle emergences from each taxon, including emergence frequencies. These are also given for the 1991 field season for taxa that were also collected in the 1992 and 1993 seasons.

Tables II and III include only longicorn taxa with a host range of 2–5 host plants. In order to emphasize patterns of host utilization, only oligophagous beetles were included as defined above and shown in Table III. Longicorn species that occur in plant families other than the Leguminosae (generalists) were omitted, as were longicorn species with insufficient data to determine their reproductive strategy. This selection facilitates the recognition of beetle guilds and patterns of host specificity. Both longicorns with a wide host range outside the Leguminosae and rare unicates are uninformative in the context of the present study. This does not mean that these rare species of longicorn don't deserve further investigation (on the contrary!); rather, at this point there are simply not enough data available on the reproductive success, distribution, and host range of these species to allow for any conclusions.

The following results and discussions of our findings are arranged in taxonomic order of the host-plant species. Species with similar beetle guilds and/or chemical patterns are grouped together: e.g., the Swartzieae are discussed as one group, and *Hymenolobium*, *Andira*, and *Acosmium* in the Sophoreae and Dalbergieae tribes of the Fabaceae as another group, because of their chemical similarities as well as their common longicorn guild. Evidence for the existence of beetle guilds—e.g., groups of mostly taxonomically unrelated longicorn species—on a group of taxonomically related host plants is provided in Table III. The visible clusters in the table clearly correspond to longicorn guilds for each tribe or group of tribes. Disjunct distributions are marked.

1. Swartzieae

The Swartzieae are represented in this study with four taxa, *Bocoa prouacensis*, *Swartzia panacoco*, *S. panacoco* var. *sagotii*, and *S. polyphylla*. Phytochemical analysis revealed that the four taxa show a very diverse chemical profile of terpenoids (vanillin-positive, nonpolar compounds) and a few UV-active, polar compounds (coumarins, phenylpropanoids, flavonoids). The polar phenylpropanoids were found in all species of Swartzieae. Literature on the chemical constituents of Swartzieae is sparse, the most prominent probably being the report of molluscicidal saponins from *S. madagascariensis* (Borel & Hostettmann, 1987) and a cytotoxic isoflavone from *S. polyphylla* (Dubois & Sneden, 1992).

Four species of long-horned beetles occur uniquely on Swartzieae: *Cycnidolon approximatum* and *Odontocera molorchoides* emerged from *Bocoa proucensis* as well as the *Swartzia* species. *Agaone notabilis* and a new species of *Odontocera* (sp. nov. 1018) emerged from all three species of *Swartzia* under investigation. Tavakilian et al. (this issue) list three other species of *Swartzia*, and the cerambycids they report confirm the beetle guild observed on the species discussed here.

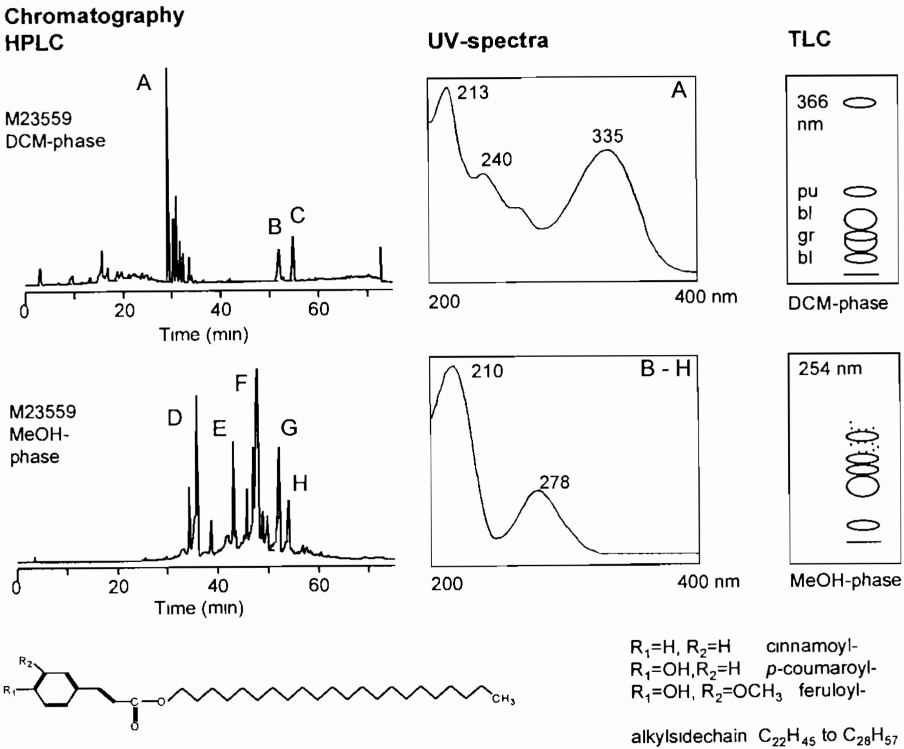
With respect to the taxonomic status of the Swartzieae, it is noteworthy that *Colobothea hirtipes*, a cerambycid otherwise found only on *Paramachaerium* and *Machaerium* of the Fabaceae tribe Dalbergieae and in *Acosmium* of the Fabaceae tribe Sophoreae, also emerged

Taxonomy

Family	Caesalpiniaceae
Tribe	Cercideae
Genus	*Bauhinia*
Species	*B. guianensis*
Collections	M23471, M23641, M 23678
Species	*B. outimouta*
Collections	M23559, M23626

Longicorn guild

Species	Tribe
Estola sp. 435	Desmiphorini
gen. sp. 951	Acanthocinini
Colobothea sp. 322	Colobotheini
Hilobothea latevittata	Colobotheini



R_1=H, R_2=H cinnamoyl-
R_1=OH, R_2=H *p*-coumaroyl-
R_1=OH, R_2=OCH_3 feruloyl-

alkylsidechain $C_{22}H_{45}$ to $C_{28}H_{57}$ (Achenbach et al., 1986, from wood of *Bauhinia manca*)

Compound A possibly feruloyl alkyl ester
Compounds B - H possibly cinnamoyl alkyl esters

Fig. 2. Wood chemistry and longicorn guilds of the genus *Bauhinia*. Major compounds in the HPLC-profiles are marked, and their UV-spectra are depicted separately. HPLC and TLC conditions are described in the text, under "Material and Methods."

from *Swartzia polyphylla*. However, *Colobothea hirtipes* was also found in families other than the Leguminosae, thus having a broad host range (Tavakilian et al., this issue). Another disjunct distribution was noted for *Odontocera* sp. nov. 1018, which was also found in two species of the Caesalpiniaceae. As this species was not observed in any other group of legumes, this could point to some chemical similarities among the Caesalpiniaceae and the Swartzieae. Although the phytochemical analysis (Table I) did not reveal any identical compounds among the host taxa of *Odontocera* sp. nov. 1018, all of its host plants show an abundance of phenylpropanoids in the polar phases (H_2O II-phase and MeOH-phase).

2. Bauhinia *(Tribe Cercideae, Caesalpiniaceae)*

Both species of *Bauhinia* investigated (*B. guianensis* and *B. outimouta*) show a similar chemical pattern consisting probably of saturated unbranched alcohols and their ferulic, *p*-coumaric acid, and possibly cinnamic acid esters, similar to those that were reported from wood of *Bauhinia manca* by Achenbach et al. (1986; also see Fig. 2).

Both *Bauhinia* species also exhibit a uniquely similar pattern of cerambycids consisting of an undescribed species of *Colobothea* (sp. nov. 322) and the extraordinarily abundant *Hilobothea latevittata.* In addition, a species of *Estola* (no. 451) and an unidentified species of the tribe Acanthocinini (no. 951) appear to utilize *Bauhinia* wood (cf. Tavakilian et al., this issue; and Table II).

Only one cerambycid, *Lissonotus equestris,* was found in another tribe of the Caesalpiniaceae, in *Macrolobium* in the tribe Amherstieae.

The *Bauhinia* group is a good example of a guild of beetles consistently correlated with evident chemical similarities in the host plants.

3. Cassieae and Caesalpinieae

Four genera belonging to the Cassieae and Caesalpinieae of the Caesalpiniaceae were investigated: *Chamaecrista, Dicorynia, Sclerolobium,* and *Vouacapoua. Dicorynia guianensis* (Cassieae) and *Sclerolobium* (Caesalpinieae) appearently share one polar aromatic compound. Other chemical patterns detected include anthraquinones in *Chamaecrista apoucouita* (Hegnauer, 1994) and dominant diterpenes and phenylpropanoids in *Vouacapoua americana.*

However, patterns of cerambycid emergences are inconclusive, consisting either of unique, rare beetles or generalists. The additional data provided in Tavakilian et al. (this issue) indicate that species of *Sclerolobium* apparently serve as host plants to several species of *Chrysoprasis* (Heteropsini) and *Eburodacrys* (Eburiini), which also occur on some Mimosaceae.

4. Detarieae and Amherstieae

The two tribes Detarieae and Amherstieae were represented by several genera: *Crudia, Eperua, Heterostemon,* and *Peltogyne* in the Detarieae, and *Macrolobium* in the Amherstieae. The two tribes are thought to be closely related (Polhill & Raven, 1981). *Crudia bracteata* and *Peltogyne venosa* were available as multiple samples. This allowed us to determine variability in beetle emergences and in chemical patterns among individuals of one species. Chemical composition appeared to be rather conserved, while some variation was found in longicorn emergences (see also Tavakilian et al., this issue).

Crudia bracteata (Detarieae), along with other species of *Crudia,* have hardly been investigated for their phytochemicals. We found abundantly nonpolar compounds in the wood samples, probably terpenoids, and one dominant aromatic compound (coumarin or other phenylpropanoid) that also occurs in *Macrolobium* and *Heterostemon.* The legume genus *Eperua* has predominantly nonpolar compounds in bark and wood, and apparently produces a diterpene-rich wood resin. *Peltogyne venosa* is characterized by its unique purple flavonoids, the peltogynols (Bisby et al., 1994), but other nonpolar terpenoids were detected. In summary, the two tribes seem to be characterized by an abundance of nonpolar compounds (likely diterpenes) and a few outstanding phenolics such as the purple flavonoid in *Peltogyne* and the phenolic in *Crudia, Heterostemon,* and *Macrolobium.* Chemical similarities were also detected between *Eperua falcata* and *Vouacapoua americana* (tribe Caesalpinieae, see above), a genus that is also reported to produce diterpenoid resins.

The data in Tavakilian et al. (this issue) show that the longicorn species *Cicatrizocera bilistrata* occurs on all species of the genus *Crudia* so far investigated. The long-horned beetle *Cosmotoma adjuncta* occurs on *Crudia* and *Macrolobium* and in the Mimosaceae. The genus *Eperua* hosts an extraordinary diversity of cerambycids, many of them occurring also on *Macrolobium*, including *Chlorida curta* and *Cycnidolon batesianum*. Noteworthy is the occurrence of the cerambycid species *Sphaerion cassum* and *Brasilianus plicatus* on both *Eperua* and *Peltogyne*. The longicorn *Macronemus antennator* emerged from three of the genera in this group (Table II). The longicorn species *Pseudaethomerus lacordairei*, *Lissonotus equestris*, and *Polyrhaphis spinosa* are frequently encountered on all Detarieae and Amherstieae studied. *Brasilianus plicatus*, *Macronemus antennator*, and *Chlorida curta* were found on several plant families outside the Leguminosae (Tavakalian et al., this issue).

In summary, the Detarieae/Amherstieae serve as host plants for an abundance of longicorn species, and many, but not all, are restricted to this group. This correlates with the rather homogeneous chemical features of the tribes.

5. *Mimosaceae*

The tribe Ingeae of the Mimosaceae is represented by numerous collections, and its species are obviously abundant and dominant trees in the Sinnamary River Basin. The species investigated belong to the genera *Abarema*, *Enterolobium*, *Inga*, and *Zygia* sensu Barneby and Grimes (1996, 1997). Two other tribes of the Mimosaceae are represented by only single species. The entire family is discussed as one group.

Interpretation of the chemical analyses of wood samples of Ingeae is hampered by the fact that hardly any phytochemical studies have been conducted on the wood of Mimosaceae. The seeds of Ingeae have been surveyed thoroughly for the occurrence of unusual nonprotein amino acids and alkaloids such as pipecolic acid derivatives and albizziine (Bisby et al., 1994), and it can be assumed that the entire family produces these compounds. Many of our samples did show Dragendorff-positive compounds that could correspond to these alkaloids. However, almost no phytochemical data are available from other plant parts. This places some difficulty on the interpretation of the chromatographic data presented here.

The entire tribe appears to be characterized by the abundance of nonpolar compounds, most likely terpenoids. This correlates with a few reports of various triterpenes including steroids and saponins (Bisby et al., 1994; Hegnauer, 1994). Simple aromatic compounds were detected in the methanol phases of most specimens examined (Rt = 69 mins). These compounds were not found in any species of *Zygia*, which produces other polar, aromatic compounds instead. Very polar compounds (to be expected in the H_2O II-phase) are almost entirely absent in the Mimosaceae. With the exception of the genus *Inga*, most wood samples also lacked tannins, as indicated by the yellow color of the crude extracts.

Many Mimosaceae are used by rare cerambycids that have been reported from only a single host-plant species (Tavakilian et al., this issue). However, there are several longicorn species that seem to be typical for the entire Mimosaceae, with only very occasional occurrences in other groups of the Leguminosae. Common longicorn species are *Hemilissa catapotia*, *Thoracibidion ruficaudatum*, and *T. striatocolle*. This is particularly evident if the data provided in Tavakilian et al. (this issue) are considered. In addition, several species of the genus *Oedopeza*, most commonly *O. ocellator*, were found. *Oedopeza ocellator* has a broad range of host plants including members of the Swartzieae, Fabaceae (*Acosmium*, *Machaerium*, *Ta-*

ralea), and even some families outside the Leguminosae. However, it is abundant only in the Mimosaceae, and is recorded there with emergences of up to 56 per log (Table II). In other host-plant species it occurs in only a small number of individuals.

In conclusion, the Mimosaceae apparently exhibit several unifying features with regard to wood chemistry and utilization by long-horned beetles. Terpenoids, pipecolic acid derivatives, and albizziine-like compounds are dominant, which correlates with a guild of unique longicorns consisting of at least six species.

6. Andira–Hymenolobium–Acosmium *Group (Tribes Sophoreae and Dalbergieae, Fabaceae)*

These three genera are currently classified in two different tribes of the Fabaceae: *Andira* and *Hymenolobium* belong to the Dalbergieae and *Acosmium* is placed in the Sophoreae (Polhill & Raven, 1981), although there has been considerable debate as to the taxonomic affinities of the closely related genera *Acosmium* and *Sweetia.*

The three genera in this group exhibit remarkable chemical similarities by possessing an abundance of polar and nonpolar compounds with distinctive UV-absorption spectra, indicating the presence of phenylpropanoids, coumarins, and flavonoids (see Table I & Fig. 3). The specimens of *Hymenolobium* and *Andira* were found to share several compounds that were not found in *Acosmium*. Although the chemical profile of *Acosmium* is slightly different, the types of compounds found are the same as in *Hymenolobium* and *Andira.* The TLC-analysis yielded several Dragendorff-positive substances in the DCM-phases of the three specimens. These were investigated further for the occurrence of quinolizidine alkaloids using GC-MS with a nitrogren-specific detector (Greinwald & Meurer-Grimes, unpubl.). The occurrence of quinolizidine alkaloids could not be verified in *Hymenolobium* and *Andira* nor in *Acosmium nitens*. Quinolizidine alkaloids of the sweetinine type were reported from other *Acosmium* species (Balandrin & Kinghorn, 1981) but were not found in our wood samples. Kinghorn and Smolenski (1981) comment that the occurrence of such complex quinolizidines is noteworthy because *Acosmium* is considered one of the primitive genera of the tribe Sophoreae.

The unexpected phytochemical similarities among the genera *Hymenolobium*, *Andira*, and *Acosmium* are corroborated by the abundant occurrence of the beetle *Acyphoderes abdominalis*. This cerambycid emerged only from these three genera (see Table II & Fig. 3; Tavakilian et al., this issue). In this case, phytochemical similarities and common beetle guilds extend across currently recognized tribal limits in the host plants. A reinvestigation of the taxonomic status of the genus *Acosmium* could perhaps reveal interesting insights into the evolution of primitive Fabaceae.

It is noteworthy that the beetle guild found on *Acosmium nitens* includes a second taxon, *Colobothea hirtipes*, which occurs on the two other Dalbergieae investigated here. This observation appears to be augmented by a few similarities in phytochemical patterns observed between other members of the Dalbergieae and *Acosmium* (see Table I). *Colobothea hirtipes*, however, is a true generalist and not even restricted to the Leguminosae.

7. Machaerium-Paramachaerium *Group*

The chemical analysis of wood from the two genera *Machaerium* and *Paramachaerium* revealed striking similarities. Both are characterized by an abundance of nonpolar, nonaromatic compounds (terpenoids) and a few polar aromatic compounds. Simple aromatic com-

Taxonomy

Family:	Fabaceae
Tribe:	Dalbergieae
Species:	*Andira coriacea*, M23646 *Hymenolobium petraeum*, M23694
Tribe:	Sophoreae
Species:	*Acosmium nitens*, M23644

Chemical profile

- dominant polar compounds are phenylpropanoids (A, B) and flavonoids
- abundance of non-polar, UV-positive compounds, possibly anthraquinones and/or benzofuranoids (C, D, F), and phenylpropanoids
- alkaloids absent

Longicorn guild

Acyphoderes abdominalis (Oliver, 1795)

male, from M23644, M23646, and M23694

HPLC-profiles of polar extracts (H_2O-phase II)

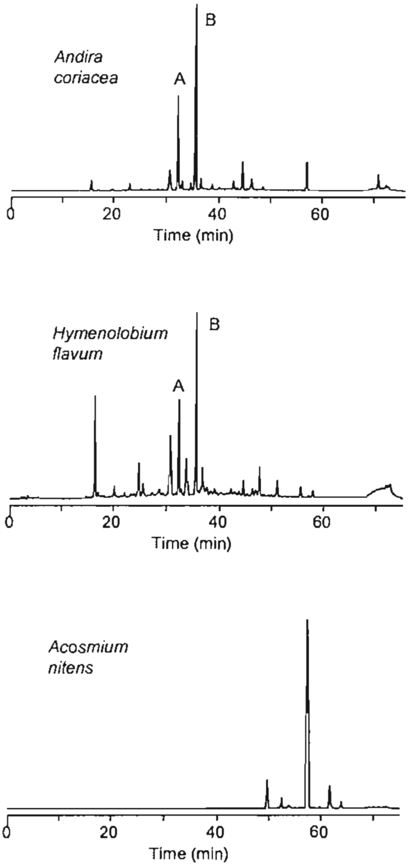
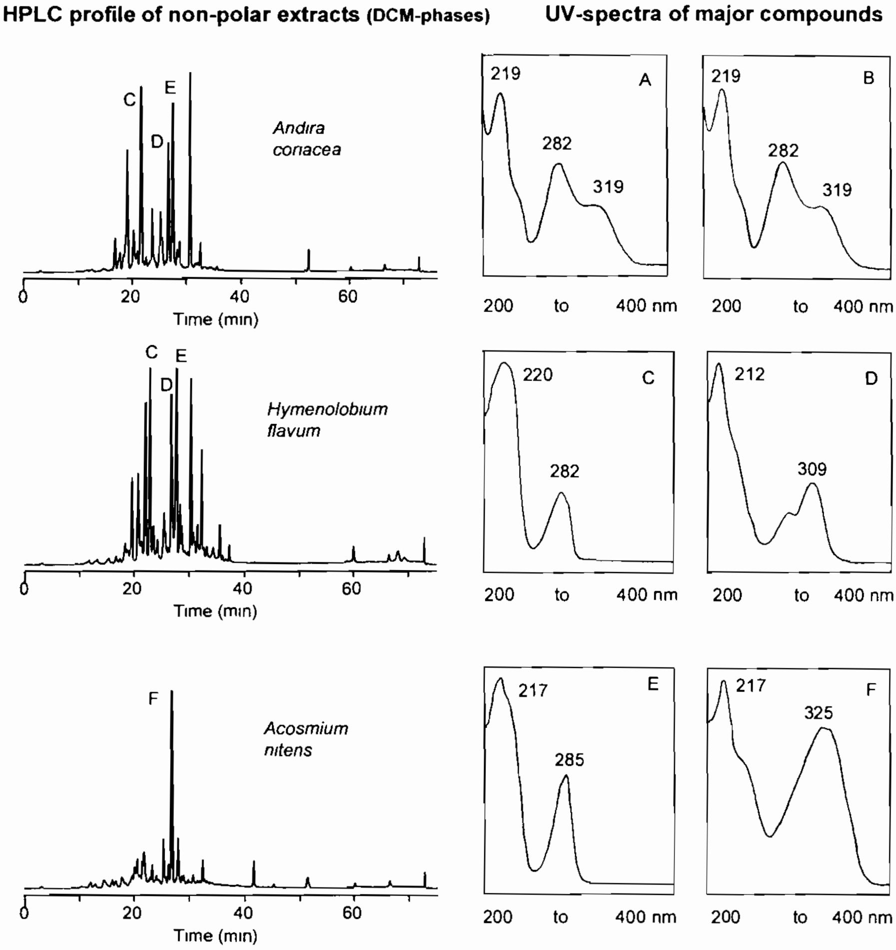


Fig. 3 (this page and facing page). Host plants of the *Acyphoderes* guild: *Andira*, *Acosmium*, and *Hymenolobium*. Prominent compounds in the HPLC-diagrams are marked with letters. The UV-absorption spectra of both polar and nonpolar compounds are depicted (facing page, far right). HPLC-conditions are described in the text, under "Material and Methods."

pounds, benzopyranoids including coumarins, stilbenes, and flavonoids, and triterpenoids have been reported from *Machaerium* (Bisby et al., 1994; Hegnauer, 1994). These two genera are distinctly different from the other two genera of Dalbergieae examined (*Andira* and *Hymenolobium*). The closely related genus *Pterocarpus* was investigated for its longicorn fauna in Tavakilian et al. (this issue), but no samples were available for phytochemical studies. Representatives of this genus are known as sandalwood and are commercially used widely. Their wood chemistry, which has been investigated rather thoroughly, seems to resemble the profiles found in *Machaerium* and *Paramachaerium*.



Machaerium and *Paramachaerium* also share the occurrence of one cerambycid species, *Colobothea hirtipes*, which also occurs on *Pterocarpus officinalis* along with other species of *Colobothea* (Tavakilian et al., this issue). As mentioned above, *Colobothea hirtipes* is rather widely distributed among the plant species examined in the Sinnamary study, but there appears a cluster of occurrences in the Dalbergieae (Fabaceae) which coincides with some phytochemical similarities in its host plants.

8. Dipteryxeae

The genera *Dipteryx* and *Taralea* belong to the Fabaceae tribe Dipteryxeae and were the only representatives of this tribe examined here.

They are phytochemically characterized by polar and nonpolar aromatic compounds such as coumarins and other benzopyranoids, the absence of alkaloids, and, at least in the case of *Taralea*, the absence of tannins.

Dipteryx and *Taralea* are utilized by one yet undescribed species of *Odontocera* (Table II), which yielded more than 100 emergences in one of the trunks! In addition, they share the common occurrence of the cerambycid *Odontocera simplex*. Therefore, this is another distinct grouping within the Fabaceae that exhibits similar phytochemical patterns and a common beetle guild.

Odontocera simplex also emerged from *Monopteryx* in the Sophoreae (Fabaceae). However, this disjunct distribution is not corroborated by chemical similarities. *Monopteryx* wood is characterized by the occurrence of alkaloids and the abundance of tannins, although simple aromatic compounds were also detected.

9. Other Fabaceae

Although several other genera in the Fabaceae were investigated (*Dioclea*, *Diplotropis*, *Dussia*, *Lonchocarpus*, *Ormosia*, *Poecilanthe*), no other longicorn guild could be established. *Diplotropis*, *Dussia*, *Lonchocarpus*, and *Ormosia* belong to the Fabaceae tribe Sophoreae, which is characterized by the presence of quinolizidine alkaloids (Bisby et al., 1994). These four genera did not reveal a common beetle guild. They seem to be characterized by the frequent occurrence of generalist longicorns such as *Nyssodrysternum* species, and *Toroneaus virens*.

E. LEGUMINOSEAE COMPARED TO OTHER PLANT FAMILIES

It is difficult to single out one chemical trait that is typical to all three legume families and distinguishes them from the other plant families investigated here. However, it is possible to list a few species of longicorns that utilize members of more than one of the three legume families but that do not occur on any plant family outside the Leguminosae. These include, for example, *Cosmotoma adjuncta*, *Cycnidolon batesianum*, several species of *Odontocera* and *Oedopeza*, *Polyrhaphis spinosa*, and *Sphaerion cassum*.

A comparison with beetle guilds listed in Tavakilian et al. (this issue) shows that most of them appear to be typical at the family level; for example, there are well-defined guilds for the Euphorbiaceae, Moraceae, and Lecythidaceae, and only rarely are members of these guilds restricted to a single genus or group of genera. The Leguminosae appear to be the only larger taxonomic group investigated so far that hosts several beetle guilds restricted to single genera, tribes, or groups of tribes of host plants as described above. However, with the exception of the Lecythidaceae, no other family has been thoroughly evaluated yet for correlations between longicorn guilds and subfamily-level taxonomy.

F. TAXONOMIC RELATIONSHIPS WITHIN LONGICORN GUILDS

The beetle guilds identified in the course of this study generally comprise taxa that are taxonomically not related to each other. For example, the cerambycid guild found on *Bauhinia* consists of four taxa (Table II & Fig. 2), most of them belonging to a different cerambycid tribe: *Colobothea* sp. nov. 322 and *Hilobothea latevittata* belong to the Colobotheini. *Estola* sp. nov. 435 appears to be the only representative of the cerambycid family Desmiphorini found on a legume host plant, and *Lissonotus equestris* is classified in the longicorn tribe Lissonotini. The beetle guild found on Swartzieae (Table II) consists of several species of Rhinotragini (*Agaone notabilis* and 2 species of *Odontocera*), one representative of Colobotheini, and one representative of Ibidionini (*Cycnidolon approximatum*). The longicorn guild found on the Mimosaceae (with only the tribe Ingeae adequately sampled here) hosts species of 15 different tribes, according to the listing in Tavakilian et al. (this issue). Dominant species are several members of the genus *Oedopeza* (Acanthocinini), two species of *Thoracibidion* (Ibidionini), and *Hemilissa catapotia* (Piezocereini).

There are very few examples of two or more closely related longicorn species occurring on closely related host plants (e.g., the two species of *Thoracibidion* on Mimosaceae). The overall pattern is, indeed, that the longicorn species belonging to one guild are not taxonomically related to each other. This has important implications for the discussion of the phylogenetic roots and ecological characteristics of these beetle guilds as discussed below.

V. Conclusions

Within the large order Leguminosae, only some taxonomic groups appear to be utilized by a consistent guild of cerambycid beetles. These groups are the Swartzieae, *Bauhinia*, Detrieae–Amherstieae, *Andira–Hymenolobium–Acosmium*, *Machaerium–Paramachaerium*, Dipteryxeae, and the family Mimosaceae. Many taxonomic groups of legume host plants are not associated with well-defined groups of cerambycids and are utilized by a few polyphagous beetles, or host only one or two rare species, e.g., the Fabaceae genera *Ormosia*, *Lonchocarpus*, and *Dioclea* or the tribes Cassieae and Caesalpinieae in the Caesalpiniaceae. The members of each beetle guild are usually not closely related species but representatives of different tribes of Cerambycidae. The plant species that constitute the hosts for these guilds usually have similar phytochemical profiles.

The fact that some groups of Leguminosae do not correlate with any longicorn guilds could be due to a number of demographic or climatic factors, and it would be premature to assume that these plant species really do not host any unique longicorn species. For example, certain beetle species may not have been present in that area at the time the trees were felled. Further studies on cerambycid behavior and life cycles are definitely needed before more targeted investigations into their host fidelity can be designed.

The evaluation of the taxonomic affiliations within beetle guilds teaches us that the patterns of host specificity are most likely the result of several different colonization events. Many different cerambycid lineages appeared to have radiated into the Leguminosae, resulting in the beetle guilds that are described in Tavakilian et al. (in this issue) and in this study. There are several other studies that have come to similar conclusions and corroborate the interpretation of our results.

Brown (1987) described the first case where patterns of host specificity in an insect–plant relationship can be explained by sequential colonization through successive chemical adaptation in the Ithominiinae butterflies and their solanaceous host plants. He found, for example, that utilization of host plants by *Mechanitis* females does not correlate with taxonomic lines of host plants and that no pattern of reciprocal evolution was evident. Overall, he observed the trend that the most advanced Ithomiinae oviposit on the most primitive host plants. In his alternative hypothesis, he explained the pattern of host specificity by assuming that one ancestral lineage of Ithominiiae had originally adapted to the Solanaceae chemistry and then radiated onto other species by progressively adapting to related phytochemical patterns. Brown also says that the Ithomiinae make mistakes in oviposition, obviously confused by similar chemical profiles of suitable and unsuitable host plants. Brown (1987; Brown et al., 1991) emphasizes that plant chemistry plays a crucial role in this form of resource allocation.

Chemical clues are used for host recognition, and a selective adaptation to host chemistry gives the insect species the monopoly on the food source.

Brown's conclusion is confirmed by our finding that the longicorn guilds are mostly restricted to chemically similar groups of host plants. For example, the two species of *Bauhinia* exhibit nearly identical chemical patterns consisting of unique aliphatic compounds and their aromatic esters (Fig. 2). The correlation between phytochemical similarities and occurrence of beetle species or guilds is particularly evident when these similarities extend across currently recognized taxonomic groupings in host plants. This is certainly the case in the *Andira–Hymenolobium–Acosmium* beetle guild discussed above (Fig. 3). It appears that chemical profiles are important in host recognition and host allocation.

This scenario of adaptive radiation is strengthened by the fact that adaptive responses to changes in chemical composition of host plants may occur extremely quickly among insects, often within a few generations of herbivores (see Bowers, 1988, for summary). This is particularly known from agricultural pest organisms and their rapid responses to insecticides. For example, more and more cases of resistance to the pyrethrins are now being reported (Cochran, 1995). These are natural polyacetylenes derived from the flowers of *Chrysanthemum coccineum* and *C. cinerariaefolium* and have been used for several decades as insecticides on farms or as mosquito deterrents. Another example can be found in the attempts to breed varieties of *Solanum tuberosum* that are naturally resistant to the Colorado potato beetle (*Leptinotarsa decemlineata*). A number of varieties have been bred with an altered content of steroidal alkaloids, but beetle populations rapidly develop the ability to tolerate the new toxins (review in Harborne, 1993). This ability to develop tolerance for previously unencountered chemicals is certainly helpful when new resources are being colonized. Recently, the biochemical basis for such extreme adaptability has been discovered in form of the P-450 monooxygenase enzymes that are found in the digestive tracts of insects and are involved in the detoxification of ingested materials (Schuler, 1996).

The pattern of cerambycid guilds consisting of taxonomically unrelated species occurring on chemically similar host plants could be the result of many events of adaptive radiation in different cerambycid lineages. It appears that the colonization patterns found within the Cerambycidae (at least on the Leguminosae) resembles the colonization patterns that can be stated for most organisms associated with a particular host plant (or group of host plants). One noted example for the existence of an herbivore guild consisting of taxonomically unrelated organisms on a group of chemically similar and closely related host plants are the butterfly weeds (genus *Asclepias*) and their specialized insect herbivores. The genus is characterized by the production of rather toxic cardiac glycosides (see Harborne, 1993, for review). It hosts a number of highly adapted herbivores, most famously the larvae of the monarch butterflies but also four other aposematic butterflies, several Lygaeid bugs, pyrgomorphid grasshoppers and beetles, and one aphid. Most of these herbivores exhibit a warning coloration, and all have apparently developed the ability to sequester the toxic cardiac glycosides and use them for their own defense purposes. Although at present no evidence has been gathered that the longicorns of tropical trees sequester the chemicals of their host plants, this cannot be excluded. Some of the brightly colored longicorns would certainly be good targets for examining sequestration of host-plant toxins. However, the important similarity between the longicorn guilds and the *Asclepias* guild is that these herbivore guilds consist of taxonomically unrelated species. This pattern appears to be the same whether the host plants are capable of reproduction—that is, capable of passing on changes in secondary chemistry to the next generation—as in *Asclepias* species, or whether the host plants are dead, as was the case in our study. In the case of our dead host plants, genetic changes in host-plant chemistry (if they occur) are definitely not the result of herbivore pressure by cerambycid larvae! This means that, while insects may very well adapt to the chemistry of their host plants, host-plant chemistry probably did not evolve in response to selection pressure generated by one single guild of herbivorous insects.

This conclusion prompts us to rethink the role of plant chemistry in the evolutionary interactions between insects and plants. To our knowledge, it has not been proven that plants actually change their profiles of secondary metabolites in response to one single predator or disease organism. Even one of the most thoroughly analyzed cases, the case of lepidoptera larvae feeding on coumarin-producing host plants (Berenbaum, 1983), cannot provide even circumstantial evidence that a change in host-plant chemistry occurred in response to herbivore pressure exerted by a single pest organism. There are lepidoptera species of several unrelated lineages that specialize on feeding on coumarin producing plants. Most species feed on plants with widely distributed hydroxycoumarins, and a few related lepidopterans on much rarer plants with linear or angular furanocoumarins. But there is actually no evidence that the evolution of the highly phototoxic angular furanocoumarins is related to the selection pressure exerted by a few adapted lepidoptera species. Angular furanocoumarins are indeed more toxic than simple coumarins, but not only to lepidopterans. They are equally more toxic to viruses, microbes, and mammals including humans, due to their photosensitivity (Harborne, 1993; Nigg & Beier, 1995; Taylor et al., 1995). However, the adapted lepidopterans do have the advantage of monopolizing a food resource. Therefore, we conclude that until further evidence is provided, we can only assume that insects rapidly adapt to secondary metabolites in their host plants but not that host-plant chemistry changes in response to insect herbivore pressure exerted by a single species or guild. Circumstantial evidence for this is that there are definitely more insect species than plant species, and perhaps even more insect species than secondary metabolites.

Plants are exposed to many different environmental challenges that range from UV-light to insect herbivores, from competition with other plants to microbial disease organisms. Secondary metabolites have been shown to play a pivotal role in all of these interactions. These secondary metabolites serve a plant species best if they have multiple activities, e.g., if they aid in deterring mammalian grazers as well as microbial attackers and, at the same time, serve as UV protectants and antioxidants. Considering the metabolic expense of producing secondary metabolites, it does not seem efficient to produce one group of chemicals for UV-protection, another group for deterring mammalian grazers, and yet another group for deterring insect predators. Related plant taxa groups often produce related compounds (although there are ample exceptions), and elaborate on one pathway rather than expressing multiple pathways; e.g., some plant families specialize in producing glucosinolates (Cruciferae), and others produce a wide array of sesquiterpene lactones (Asteraceae) or benzylisoquinoline alkaloids (Magnoliideae). This scenario implies that the secondary metabolites that are preferentially produced in one group have to serve multiple purposes, have multiple activities. In particular, the selection pressure exerted by microbial disease organisms on plants has hardly been investigated. Multiple biological activities of a single secondary plant metabolite has indeed been documented, especially in recent years through extensive pharmaceutical screening programs that are currently conducted by academic and industrial institutions. The quest for new medicines against virtually every human ailment, be it viral, bacterial, fungal, or protozoal in nature, has led scientists to investigate the most abundant resource of novel chemical prototypes: higher plants. However, due to the abundance of side effects, few of these screening programs have yielded compounds suitable for human use (Mendelsohn & Balick, 1995; pers. obs.). The mere existence of these side effects—a compound with promising cytostatic activities is at the same time antibacterial, or compounds with antiviral activity are at the same time cytotoxic—should give us a hint that these secondary plant metabolites probably evolved in response to a multitude of environmental challenges. In the evolution of the diversity of secondary metabolites, compounds with multiple activities were obviously favored over compounds with single activities. Compounds without side effects appear to be the rare exception rather than the rule.

Resistance against any of the multipurpose secondary metabolites can, of course, develop in any of the potential predator or disease organisms. The results of this are small guilds of adapted and tolerant but taxonomically unrelated organisms on each plant, each one of them utilizing the host plant in a different manner—a perfect system of securing resources. The longicorn guilds on tropical trees are just one of many examples.

VI. Summary

Eighty wood samples representing 51 taxa in 33 genera of Leguminosae were collected in the Sinnamary River Basin in northern French Guiana and evaluated for their fauna of long-horned beetles (Cerambycidae) and their phytochemical constituents. The phytochemical analysis (TLC, HPLC) revealed that taxonomically related taxa are mostly characterized by similar phytochemical patterns. The following, phytochemically similar groups of plant taxa host characteristic beetle guilds: Swartzieae (here treated as tribe *incertae sedis*), *Bauhinia* (Caesalpiniaceae), Detarieae–Amherstieae (Caesalpiniaceae), *Andira–Hymenolobium–Acosmium* (tribes Sophoreae and Dalbergieae, Fabaceae), *Machaerium–Paramachaerium* (Dalbergieae, Fabaceae), Dipteryxeae (Fabaceae), and the family Mimosaceae. Many groups of legume host plants were not found to be associated with well-defined longicorn guilds in this investigation. The members of each longicorn guild were found not to be taxonomically related. Therefore, it appears that many different cerambycid lineages have radiated into the Leguminosae during several colonization events. Our data may be used to analyze the role of plant chemistry in plant–insect interactions that are the result of adaptive radiation rather than parallel cladogenesis. It is hypothesized that the secondary metabolite composition in the wood of the host plants plays a pivotal role in resource allocation among those longicorn guilds.

VII. Acknowledgments

Our special thanks are to Amy Berkov for valuable discussions and comments on various stages of the manuscript. Technical assistance was provided by Betsey Hallihan, Ivelisse Rovira, Carey Mitchell, and Andrew Amo (AA funded by NIH grant No. 2S03RR03421-10, Minority High School Student Research Apprentice Program, Lehman College). We thank Roland Greinwald for the GC-MS analysis of several wood extracts, and James Grimes for discussions on the taxonomy of Leguminosae. The project was funded by PSC-CUNY awards No. 664482, 666193, and 667192 from The City University of New York to BMG, and a grant from Electricité de France to GT.

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