A comparison of hispine beetles (Coleoptera: Chrysomelidae) associated with three orders of monocot host plants in lowland Panama

Christophe Meskens[1]*, Donald Windsor[2] and Thierry Hance[1]

[1]Unité d'Écologie et de Biogéographie, Biodiversity Research Centre, Université catholique de Louvain, 4-5, Place Croix du Sud, Louvain-la-Neuve 1348, Belgium: [2]Smithsonian Tropical Research Institute, Apartado 0843-03092, Panama

Abstract. The feeding traces in fossil ginger leaves and the conserved phylogenetic relationships seen today in certain clades of hispine beetles on their monocot hosts point towards a long and intimate plant–insect evolutionary relationship. Studies in the 1970s and 1980s documented the rich fauna of rolled-leaf hispine beetles and their association with the Neotropical monocot family Heliconiaceae in Central America. In this report, the taxonomic breadth of these early studies is expanded to include species in the families, Marantaceae, Poaceae, Arecaceae and Costaceae, all with species occurring sympatrically with the Heliconiaceae in lowland Panama. Additionally, the analysis is widened to include open-leaf scraping and internal leaf-mining clades of hispoid Cassidinae. The censuses add more than 5080 Cassidinae herbivore occurrence records on both open and unfurled new leaf rolls of 4600 individual plants. Cluster analysis reveals that while many Hispinae species tend to group with plant species in only one of the three monocot orders, 9 of 16 Hispinae species on Zingiberales hosts were recorded in substantial numbers on both the Heliconiaceae and the Marantaceae, indicating an underlying pattern of feeding flexibility at the host plant family level.

Key words: Cassidinae, Arecales, Poales, Zingiberales, hispine beetles, species assemblages

Introduction

Interactions among plants and phytophagous insects play a key role in community function and evolution. Trophic relationships provide useful insights into understanding important community dynamics (Chave, 2004). Relationships with host plants and food specialization that evolved in the past may shape contemporaneous communities and species assemblages (Novotny *et al.*, 2002). Diet and degree of food specialization are poorly characterized for many tropical phytophagous insects, including many species of hispine beetles (Coleoptera: Chrysomelidae: Cassidinae), a group distributed worldwide containing approximately 3000 species distributed among 24 tribes and 170 genera (Staines, 2002). The relationships between selected groups of host plants and their phytophagous insects can provide insights into the evolution of feeding associations and their phylogenetic constraints (Dobler *et al.*, 1996). Such an approach

---

* E-mail: cmeskens@yahoo.fr; Hance@ecol.ucl.ac.be

requires sampling a large number of potential host plant species during consecutive seasons for an entire guild of the phytophagous insects. Our study compares the assemblages of hispine beetle species associated with five families of monocotyledonous plants, Heliconiaceae, Marantaceae and Costaceae (Zingiberales), Poaceae (Poales) and Arecaceae (Arecales) in a single geographical area, the lowland Neotropical forests of central Panama.

The diverse New World hispine beetles include 11 tribes, among which Cephaloleiini or 'rolled-leaf hispines' have cryptophagic larvae and are largely associated with three orders of plants, Poales, Arecales and Zingiberales (Jolivet, 1997). Feeding grooves in fossilized ginger leaves of late Cretaceous age suggest that the Cephaloleiini clade of hispine beetles may have had a long and intimate plant–insect evolutionary relationship with their monocot hosts (Wilf *et al.*, 2000). The hispine tribes, Chalepini and Sceloenoplini, have endophagic or 'leaf-mining' larvae and are associated with a diverse set of both monocotyledonous and dicotyledonous host plant families (Hespenheide and Dang, 1999). The Hemisphaerotini, a relatively small tribe of putative hispines, have exophagic larvae and are associated principally with the New World monocotyledonous orders: Pandanales (Cyclanthaceae) (D. Windsor, personal communication), Poales (Bromeliaceae) (D. Windsor, personal communication), Arecales and Zingiberales. Aspects of the natural history and ecology of these three groups are discussed in Jolivet (1997), Strong (1977a,b, 1983), Chaboo and Nguyen (2004) and Chaboo (2007). Thus, with the exception of some genera of leaf-mining hispines, the vast majority of taxa are associates of basal angiosperms in the Monocotyledonae (Soltis *et al.*, 2005). A basal position for several hispine taxa within the Cassidinae subfamily was indicated in an early phylogenetic reconstruction using a fragment of the 12S ribosomal mtDNA gene (Hsiao and Windsor, 1999) and in a subsequent morphological study (Chaboo, 2007). With only minor exceptions, both adult and larval hispines feed on the same host plant species (Jolivet, 1997). Previous studies of hispine beetles examined communities associated with a single monocot genus *Heliconia* (Seifert and Seifert, 1976; Seifert, 1982; Strong, 1977a,b, 1982, 1983; Staines, 2002). The actual host plants of more than 70% of hispine genera are still unidentified or poorly supported (Jolivet, 1997). In this paper, we present additional data on the assemblage of hispine species associated with *Heliconia* species and we compare those to the hispine assemblages occurring on other species of monocots in the same habitat. Because the term 'community' when referring to a collection of hispine species can be misleading or ambiguous (Strong, 1977b, 1982), we use the term 'species assemblage' (Allaby, 2003) in this paper to refer collectively to all hispine species occurring on a specified set of host plants.

The summary trees of commelinoid phylogeny (Janssen and Bremer, 2004; Soltis *et al.*, 2005) indicate that the Arecaceae is the older plant family in our study, splitting off from the core monocots before the Poaceae and the Zingiberales. The Heliconiaceae branched from Zingiberales stock earlier than the Costaceae and these earlier than the Marantaceae. Janssen and Bremer (2004) showed that these three phylogenetically separated families of Zingiberales often co-occur in the understorey of Neotropical forests. Williams and Harborne (1977) reported substantial differences in flavonoid content between these three Zingiberales families. The Marantaceae and Heliconiaceae are the most abundant Zingiberales in many lowland areas of Central America (Seifert and Seifert, 1976; Seifert, 1982; Strong, 1977a,b, 1982; Flowers and Janzen, 1997). Our study examines the hypothesis that hispine beetles will share structurally similar species of plants occurring in the same or nearby habitats. An alternative hypothesis is that hispine beetles will share plants having similar histories of diversification. That is, flowering plants may have shaped beetle diversification leaving host plant associations at the family level as an enduring record of this process. In particular, older plant families such as the Arecaceae (Soltis *et al.*, 2005) are expected to support more diverse faunas and more basal taxa than are found on younger families such as the Marantaceae. Our study also examines Strong's contentions that broadly distributed Zingiberales food plants will have more associated hispine species than narrowly distributed ones and that a plant species will have a constant number of associated hispines throughout its range but that the particular species may change according to location ('geographical replacement') (Strong, 1977b, 1982).

Materials and methods

Study area, host plants and sampling method

Observations were made within forests along the east bank of the Panama Canal including a site near Gamboa in Parque Natural Soberania (9°7'N, 79°42'W), along the trail system on Barro Colorado Island (9°9'N, 79°51'W) and within the Parque Metropolitano (8°59'N, 79°33'W; near Panama City). Observations were made during 18 total months within both dry and wet seasons between May 2002 and July 2006.

Our study is based on observations recorded from a total of 17 species of monocot host plants (Table 1). Twelve of these species are within the

order Zingiberales and included six species of Heliconiaceae, five species of Marantaceae and one species of Costaceae. Species within these families, all native to the Neotropics (Croat, 1978), are characterized by large and colourful bracts and by young leaves rolled into long tubes opening after the periods from a few days to a few weeks into large mature leaves with transverse venation, long petioles and high-flavonoid content (Berry and Kress, 1991). The scroll-like immature leaves are the typical habitat for 'rolled-leaf' hispoid Cassidinae (Strong, 1983; Jolivet, 1997). This study additionally includes four species of the Arecaceae whose young leaflets initially form relatively compact sword-like structures, which subsequently begin to open and provide habitat for hispines as the leaf expands to full size. Finally, the study includes one species of the Poaceae (*Chusquea simpliciflora* Munro) whose new leaves are rolled at the base.

Ecologically, these five families occur in a range of habitats from old forest to human-disturbed areas. We classified each species into one of seven habitat categories according to the information given by Croat (1978) and Kress (1990) (Table 1). Host plant species were chosen because of their abundance in the study sites (Croat, 1978; personal observations) and the presence of a diversified

hispoid Cassidinae fauna (Strong, 1977a,b; Staines, 2004; D. Windsor, personal communication). Thus, the study lacks data from rare host plant taxa and those taxa that are rarely or never fed upon by hispines. While the host plant species are all part of the native flora of Panama (Croat, 1978), all of them occur elsewhere in Central and South America (Table 1).

We recorded the number of leaves unrolled or expanded for each individual plant that was sampled and the number of species and developmental stage (egg, larva and pupa) for hispine beetles observed or collected. Plants occurring along trails were surveyed inside young (60- to 120-year-old) and old (400-year-old) forests on BCI and along trails in mainland forests (Parque Soberania and Parque Metropolitano). Hispine species were identified based on the plates in the Biologia Centrali-Americana (Baly, 1885–1894), descriptions and key given by Staines (1996, 2002) and by comparison to identified specimens in the STRI insect collection. Beetles species were normally easily identified in the field but were collected when their identification was in doubt, as with leaf-miner larvae which were reared in the laboratory to obtain and identify the adults. Study sites were visited once a week during the sampling

Table 1. Host plant characteristics and numbers of each plant species sampled

Host plant family and species	Range[1]	Habitat[2]	Size[1]	No.
Arecaceae				
Bactris major Jacq.	Panama	Understorey (forest)	8 m	172
Chamaedorea wendlandiana Hemsl.	Nicaragua to Panama	Understorey (forest, near streams)	Up to 5 m	358
Cryosophila warscewiczii Bartl.	Belize to Colombia	Understorey (younger forest)	Up to 10 m	196
Oenocarpus panamanus Bailey	Costa Rica and Panama	Understorey (forest)	8–20 m	289
Costaceae				
Costus pulverulentus Presl	Mexico to Ecuador	Old tree-fall gap	0.5–3.5 m	63
Heliconiaceae				
Heliconia catheta R. R. Smith	Panama	Tree-fall gap	3–5 m	156
Heliconia irrasa R. R. Smith Lane	Mexico to Colombia	Understorey (forest)	1.5–2 m	242
Heliconia latispatha Benth.	Mexico to South America	Disturbed area	1.5–3 m	±740
Heliconia mariae Hook	Belize to Panama	Understorey (forest)	3–6 m	82
Heliconia vaginalis Benth.	Mexico to Ecuador	Tree-fall gap	1–3 m	125
Heliconia wagneriana O. G. Petersen	Honduras to Panama	Clearings	Up to 6 m	39
Marantaceae				
Calathea inocephala Kenn. & Nic.	Mexico to Peru	Understorey (forest)	2–4 m	831
Calathea insignis O. G. Petersen	Mexico to Peru	Tree-fall gap	2–3 m	227
Calathea latifolia Klotzsch	Venezuela to Panama	Disturbed area	1–2 m	452
Calathea lutea Schult.	Mexico to Peru	Tree-fall gap	2–3 m	51
Ischnosiphon pruinosus O. G. Petersen	Belize to Panama	Tree-fall gap	2–3 m	247
Poaceae				
Chusquea simpliciflora Munro	Guatemala to Panama	Forest	Up to 25 m	±400

Range, distribution area; No., number of visited individuals per host plant species in the present study.
[1] Croat (1978).
[2] Croat (1978) and Berry and Kress (1991).

periods. Because leaf rolls and mined leaves had to be destructively removed, each individual plant was surveyed only once a field season to minimize disturbance to beetle assemblages. The scroll-like immature leaves were only included in the study if they were closed at the bottom (watertight) thereby maintaining a high degree of humidity, which appeared to be an important factor for 'rolled-leaf' Cassidinae communities (Strong, 1977a). A set of voucher specimens was deposited in the collections of the Smithsonian Tropical Research Institute in Panama.

Statistical analysis: species richness and community analysis

Hispine species accumulation curves for each host plant species were generated using five different estimators: Chao 1, Chao 2, Jacknife 1, Jacknife 2 and Bootstrap (Species Diversity and Richness, Version 3.0, Pisces Conservation Ltd, 2002b). The sampling of hispine species was considered exhaustive when the species accumulation curve for that plant species approached an asymptote. The faunas of two species, *Costus pulverulentus* Presl and *Heliconia vaginalis* Benth., did not reach an asymptote indicating further sampling is warranted for these species.

To determine whether factors proposed by Strong (1977a,b) had a significant impact on Cassidinae species richness and average abundance per plant, we performed a Kruskal–Wallis one-way ANOVA (Systat, Version 10, SPSS Inc., 2000). This analysis was applied independently to six matrices (three factors: plant size (height: <3 m or >3 m), plant habitat (forest and understorey or disturbed) and plant range (Central America or Central America plus South America); two variables (richness and average abundance). The sampling effort was not constant for each plant species; therefore, we normalized herbivore species occurrence data by dividing the number of hispine individuals observed on a particular host plant species by the number of individuals of that plant species surveyed. To define the hispine species assemblages associated with each host plant species, we applied 'average linkage' method and Bray–Curtis' distance clustering to normalized field data, procedures widely used in ecological studies with species abundance. The cluster analysis allows identifying a set of groups (hispine assemblages), which both minimize within-group variation and maximize between-group variation (Dufrêne and Legendre, 1997; Legendre and Legendre, 1998; Community Analysis Package, Version 2.0, Pisces Conservation Ltd, 2002a).

Results

More than 4670 host plant individuals (17 species) were inspected (Table 1) and 5080 hispoid Cassidinae individuals were collected or identified in place (1013 on five species of Marantaceae, 1072 on six species of Heliconiaceae, 11 on one species of Costaceae, 36 on one species of Poaceae and 2948 on four species of Arecaceae). The host plant species were classified into seven habitats and had ranges varying from Mexico to South America (Table 1). The Cassidinae observed in this study belonged to 30 species distributed among 11 genera (Table 2). Two Cassidinae species are apparently undescribed and were assigned provisional morphospecies names (*Cephaloleia* sp61 and *Spaethiella* sp47).

Hispine species richness per plant species ranged from 1 to 12 species (median number of hispine species per host = 5) (Fig. 1). The plant species with the richest assemblages of hispines were *Heliconia latispatha*, *H. catheta* and *Calathea latifolia* with 12, 10 and 9 species, respectively. The smallest assemblages were found on *Cryosophila warscewiczii*, *C. simpliciflora* and *H. vaginalis* with 1 (*Prosopodonta dorsata*), 3 and 3 species, respectively. At the family level, the average richness of hispines was 7.8 for Heliconiaceae, 5.8 for Marantaceae, 4 for Costaceae, 3 for Poaceae and 2.5 for Arecaceae. The numbers of hispine species associated with Heliconiaceae and Marantaceae species were not significantly different (Mann–Whitney $U = 19.0$, $P = 0.457$, df = 1).

Neither host plant habitat, host plant range nor the average size of host plants had a significant effect on hispine richness (host plant habitat: Mann–Whitney $U = 29.5$, $P = 0.53$, df = 1; plant range: Mann–Whitney $U = 47.5$, $P = 0.26$, df = 1; plant size: Mann–Whitney $U = 49.5$, $P = 0.19$, df = 1) or on hispine abundance (host plant habitat: Mann–Whitney $U = 42.0$, $P = 0.56$, df = 1; plant range: Mann–Whitney $U = 51.0$, $P = 0.15$, df = 1; plant size: Mann–Whitney $U = 30.0$, $P = 0.56$, df = 1).

Ten well-defined hispine species groups (containing a total of 30 species) were arranged by cluster analysis (average linkage method; Bray–Curtis' distance) (Fig. 2). The first dichotomy in the output separates the hispine species clusters associated with the Zingiberales from those associated with the Poales + Arecales. The next branching within the Zingiberales separates the hispines associated with the three Zingiberales families, Marantaceae, Heliconiaceae and Costaceae. The second branching of the Poales + Arecales separates these two orders. Each hispine species fell within only one cluster group (Table 3). Two hispine species, *C. stevensi* and *D. panamensis*, clustered only with themselves and diverged early in the statistical output (Fig. 2).

Table 2. The list of hispine species observed in the present study ($n = 30$), species abbreviations used in the cluster analysis (Fig. 2), and species feeding habits and larval morphologies (Strong, 1977a,b, 1983; Staines, 1996, 2002, 2004; D. Windsor pers. commun.)

Hispine species	Code	Habitat	Larvae shape	Dorsal shield	Adult habitat
Arescini					
Chelobasis bicolor Gray	Ch.bic	Rolled leaf	Onisciform	None	Rolled leaf
C. perplexa Baly	Ch.per	Rolled leaf	Onisciform	None	Rolled leaf
Cephaloleiini					
Aslamidium semicircularum Olivier	As.sem	Open leaf	Onisciform	None	Open leaf-upper side
Cephaloleia belti Baly	Ce.bel	Rolled leaf	Onisciform	None	Rolled leaf
C. costaricensis Uhmann	Ce.cos	Rolled or open leaf	Onisciform	None	Rolled leaf
C. dilaticollis Baly	Ce.dil	Rolled leaf	Onisciform	None	Rolled leaf
C. dorsalis Baly	Ce.dor	Rolled leaf	Onisciform	None	Rolled leaf
C. erichsonii Baly	Ce.eri	Rolled leaf	Onisciform	None	Rolled leaf
C. instabilis Baly	Ce.ins	Rolled leaf	Onisciform	None	Rolled leaf
C. lata Baly	Ce.lat	Rolled or open leaf	Onisciform	None	Rolled leaf
C. metalescens Baly	Ce.met	Rolled leaf	Onisciform	None	Rolled leaf
C. partita Weise	Ce.par	Rolled leaf	Onisciform	None	Rolled leaf
C. pretiosa Baly	Ce.pre	Rolled leaf	Onisciform	None	Rolled leaf
C. sallei Baly	Ce.sal	Rolled leaf	Onisciform	None	Rolled leaf
C. stevensi Baly	Ce.ste	Rolled leaf	Onisciform	None	Rolled leaf
C. suturalis Baly	Ce.sut	Rolled leaf	Onisciform	None	Rolled leaf
C. trimaculata Baly	Ce.tri	Rolled leaf	Onisciform	None	Rolled leaf
C. sp61	Ce.sp61	Rolled or open leaf	Onisciform	None	Rolled leaf
Imatidium thoracicum Fabr.	Im.tho	Open leaf	Onisciform	None	Open leaf-lower side
Homalispa nevermanni Uhmann	Ho.nev	Rolled leaf	Onisciform	None	Rolled or open leaf
Chalepini					
Platocthispa emorsitans Baly	Pl.emo	Leaf miner	Onisciform	None	Open leaf
Delocraniini					
Delocrania panamensis Champion	De.pan	Open leaf	Onisciform	Detritus	Open leaf-lower side
Hemisphaerotini					
Spaethiella circumdata Boheman	Sp.cir	Open leaf	Eruciform	Exuvial-fecal shield	Open leaf
S. marginata Champion	Sp.mar	Open leaf	Eruciform	Exuvial-fecal shield	Open leaf
S. tristis Boheman	Sp.tri	Open leaf	Eruciform	Exuvial-fecal shield	Open leaf
S. sp47	Sp.47	Open leaf	Eruciform	Exuvial-fecal shield	Open leaf
Imatidiini					
Stilpnaspis panamensis Borowiec	St.pan	Rolled or open leaf	Onisciform	None	Open leaf
Prosopodontini					
Prosopodonta dorsata Baly	Pr.dor	Open leaf	Onisciform	Urogomphus	Open leaf
Spilophorini					
Calyptocephala antennata Spaeth	Ca.ant	Open leaf	Onisciform	Exuvial shield	Open leaf
Calyptocephala brevicornis Boheman	Ca.bre	Open leaf	Onisciform	Exuvial shield	Open leaf

'Onisciform' larvae are flattened with extended segmental margins contacting the substrate, approximately oval in shape when viewed from above, while 'eruciform' larvae are circular in cross section, their mass largely supported by their legs and they are tubular shaped.
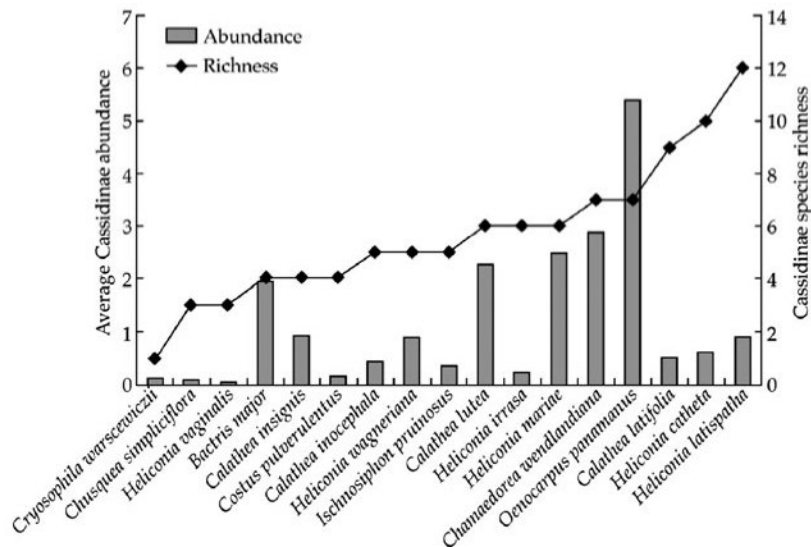
Fig. 1. Hispine species abundance (the average number of hispine individuals observed per plant) and richness (number of hispines species per plant species) on 17 species of monocotyledonous host plants

Discussion

This study represents the first large-scale survey of hispoid Cassidinae on the Isthmus of Panama. Thirty species of hispoid Cassidinae were encountered on leaves of more than 4670 individual plants in five monocotyledonous families (Table 4). When normalized by number of individuals per host plant species, the occurrence data suggest that strong preferences exist within the hispoid Cassidinae at the host plant ordinal level but less so at the familial and generic levels. Only one hispine species *Spaethiella tristis* was found on more than one plant order (Poales and Arecales), while 12 hispine species were found on more than
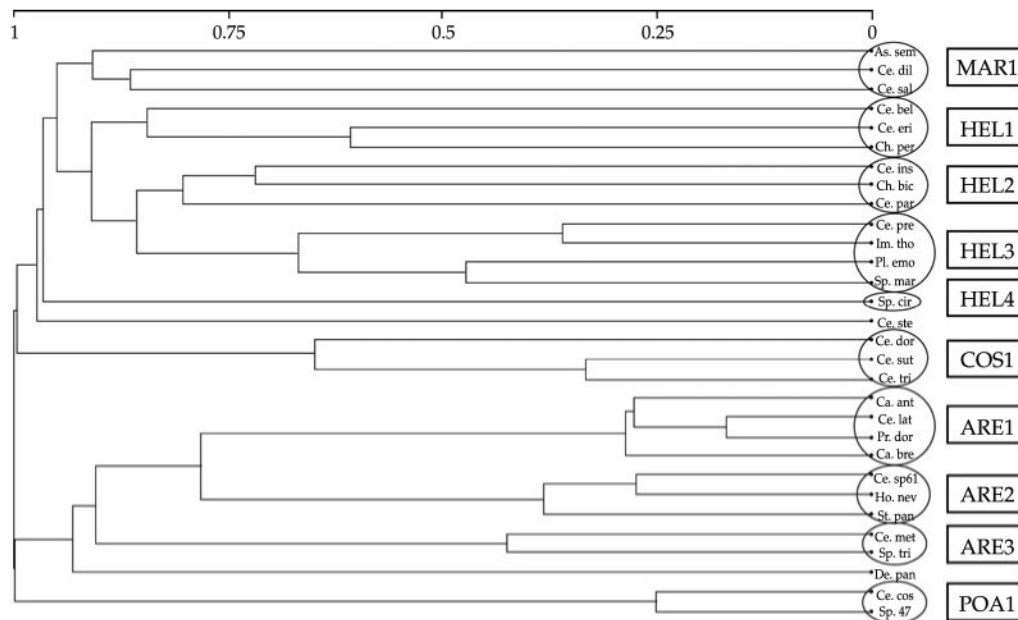

Fig. 2. Cluster analysis: Dendrogram of hispoid Cassidinae species (average linkage method; Bray–Curtis' distance). ARE1, first cluster group of Arecaceae; ARE2, second cluster group of Arecaceae; ARE3, third cluster group of Arecaceae; HEL1, first cluster group of Heliconiaceae; HEL2, second cluster group of Heliconiaceae; HEL3, third cluster group of Heliconiaceae; HEL4, fourth cluster group of Heliconiaceae; COS1, cluster group of Costaceae; MAR1, cluster group of Marantaceae; POA1, cluster group of Poaceae

Table 3. Results of cluster group analyses (dendrogram; average linkage method; Bray–Curtis' distance)

Code for cluster groups	Included host plant species	Habitat	Hispine species[+]
ARE1	*Chamaedorea wendlandiana*	Understorey (forest, near streams)	Ca.ant, Ce.lat, Pr.dor, Ca.bre
ARE2	*Cryosophila warscewiczii*	Understorey (younger forest)	Ce.sp61, Ho.nev, St.pan
	Oenocarpus panamanus	Understorey (forest)	
ARE3	*Bactris major*	Understorey (forest)	Ce.met, Sp.tri
COS1	*Costus pulverulentus*	Old tree-fall gap	Ce.dor, Ce.sut, Ce.tri
HEL1	*Heliconia mariae*	Forest	Ce.bel, Ce.eri, Ch.per
HEL2	*Heliconia catheta*	Tree-fall gap	Ce.ins, Ch.bic, Ce.par
	Heliconia vaginalis	Tree-fall gap	
	Heliconia wagneriana	Clearings	
HEL3	*Heliconia latispatha*	Highly disturbed area (anthropic)	Ce.pre, Im.tho, Pl.emo, Sp.mar
HEL4	*Heliconia irrasa*	Understorey (forest)	Sp.cir
MAR1	*Calathea inocephala*	Understorey (forest)	As.sem, Ce.dil, Ce.sal
	Calathea insignis	Tree-fall gap	
	Calathea latifolia	Disturbed area	
	Calathea lutea	Tree-fall gap	
	Ischnosiphon pruinosus	Tree-fall gap	
POA1	*Chusquea simpliciflora*	Forest	Ce.cos, Sp.47

Habitat, plant species habitat (Croat, 1978; Berry and Kress, 1991). ARE1, first cluster group of Arecaceae; ARE2, second cluster group of Arecaceae; ARE3, third cluster group of Arecaceae; HEL1, first cluster group of Heliconiaceae; HEL2, second cluster group of Heliconiaceae; HEL3, third cluster group of Heliconiaceae; HEL4, fourth cluster group of Heliconiaceae; COS1, cluster group of Costaceae; MAR1, cluster group of Marantaceae; POA1, cluster group of Poaceae.
[+] See Table 2 for hispine species abbreviations.

one plant family. No hispine species were found to be randomly distributed among host plant families, genera or host plant species (Fig. 2).

While several factors have been suggested to influence hispoid Cassidinae richness on particular host plant species (Strong, 1977a, b), our study does not support either host plant size, range or habitat type as factors significantly affecting either richness or abundance. However, it is possible that some or all of these factors working in combination could explain the high richness of the hispine assemblage associated with *H. latispatha*. This species has 12 hispine species (4 open-leaf scrapers, 1 leaf miner and 7 'rolled-leaf' hispines), and the largest range of the 17 plant species in the study. It is of moderate to large size, frequents forest margins and occurs in dense patches. Moreover, each of the three richest plant species *C. latifolia*, *H. catheta* and *H. latispatha* occurs in disturbed areas and tree-fall gaps (Table 1). Differences among species in major chemical content at the family level as described by Williams and Harborne (1977) could also contribute to the differences in hispine richness we observed among plant species. Seasonality in the production of rolled leaves is another factor that could affect species richness. The Heliconiaceae (Croat, 1978) produce young rolled leaves throughout the year while other plant families may be more seasonal in the production of rolled leaves. The Heliconiaceae thus may offer a more stable habitat than the other understorey species and thereby attract and retain more 'rolled-leaf' hispine colonists (Fig. 1). The inclusion of only four Arecales species in the study, two of which had very low-hispine richness and two of which had moderate-to-high hispine richness, makes any conclusion about the importance of the phylogenetic 'age' of this family premature.

Strong (1977a,b, 1982) recorded 12 'rolled-leaf' hispoid Cassidinae species occurring on *Heliconia* spp. in different areas in Central America while we found nine 'rolled-leaf' species in Panama (Table 2). However, only three of these species *Cephaloleia instabilis*, *Chelobasis bicolor* and *C. perplexa* occur on the same host plant species (Table 2). The difference in these faunas (Table 2) does suggest that considerable geographical replacement of hispine species in *Heliconia* communities may occur across Central America.

The results of our study also suggest that host plant data are under reported in the literature, possibly a product of sampling a narrower range of plant families and hispine tribes (Jolivet, 1997; Fernandez and Hilker, 2007). Laboratory feeding trials will be essential to know just how accurately occurrence data as presented in this study reflect actual feeding habits of hispines (Descampe *et al.*, 2007, in press).

Cluster analysis shows that hispine assemblages (Figs 2 and 3) are primarily determined by host plant affiliation (order and family) and secondarily by plant habitat. *H. latispatha* and *C. latifolia*, which occur in similar habitats, present clearly distinct

Table 4. Hispine occurrence data from the present study and that reported by previous studies

Hispine species	Host plant in present study	No.	McKenna[1]	Staines[2]	Strong[3]
Aslamidium semicircularum	*Calathea inocephala*	113	–	Zingiberales	–
	Calathea insignis	180			
	Calathea latifolia	32			
	Calathea lutea	102			
	Heliconia latispatha	1			
	Ischnosiphon pruinosus	79			
Calyptocephala antennata	*Chamaedorea wendlandiana*	286	–	–	–
	Oenocarpus panamanus	10			
Calyptocephala brevicornis	*C. wendlandiana*	197	–	–	–
Cephaloleia belti	*C. latifolia*	4	*Heliconia* sp. – PA	*Heliconia imbricata* – CR	
	C. lutea	2	*H.* sp. – CR	***H. latispatha***	
	I. pruinosus	1		*Heliconia pogonantha*	
	Heliconia catheta	47		***Heliconia mariae***	
	Heliconia irrasa	5		*Heliconia tortuosa*	
	H. latispatha	101			
	H. mariae	85			
	Heliconia wagneriana	13			
C. costaricensis	*Chusquea simpliciflora*	12	–	–	–
C. dilaticollis	*C. inocephala*	86	***C. lutea*** – PA	***C. insignis*** – CR	–
	C. insignis	4	*Calathea* sp. – PA		
	C. lutea	2	*Calathea* sp. – EC		
	I. pruinosus	1	*Renealmia* sp. – EC		
C. dorsalis	*Costus pulverulentus*	7	*Renealmia* sp. – EC	*Costus* sp. – CR	–
C. erichsonii	***C. inocephala***	186	*Calathea gymnocarpa* – CR	*C. gymnocarpa* – CR	–
	C. insignis	1	*Calathea* sp. – CR	***C. inocephala***	
	C. latifolia	4	*Heliconia* sp. – CO	*Calathea leucostachys*	
	C. lutea	3	*Calathea* sp. – PA		
	H. catheta	1			
	H. latispatha	5			
	H. mariae	70			
	Heliconia vaginalis	1			
C. insignis	*C. latifolia*	1	*H. wagneriana* – CR	***H. latispatha***	*Heliconia platystachys* – PA
	H. catheta	1		*H. imbricata*	***Heliconia curtispatha*** – PA
	H. latispatha	38		*H. wagneriana*	***H. latispatha*** – PA
	H. mariae	2			***H. latispatha*** – CR
					H. wagneriana – CR
C. lata	*C. wendlandiana*	195	*Chamaedorea tepejilote*	–	–
C. metalescens	*Bactris major*	215	Unknown – CR	–	–
	C. wendlandiana	4			
C. partita	*C. latifolia*	2	***H. latispatha*** – PA	*Heliconia* sp.	–
	H. catheta	2	*Heliconia* sp. – PA		

Table 4. *Continued*

Hispine species	Host plant in present study	No.	McKenna[1]	Staines[2]	Strong[3]
	H. latispatha	1			
C. pretiosa	C. pulverulentus	1	*Heliconia* sp. – CO	–	–
	H. catheta	12			
	H. latispatha	50			
	H. mariae	12			
	H. wagneriana	8			
Cephaloleia sallei	C. inocephala	1	H. irrasa – CR	Heliconia sp. – CR	–
	C. latifolia	168		Renealmia strobilifera	
	C. lutea	4			
	I. pruinosus	4			
	H. catheta	1			
	H. latispatha	11			
	H. mariae	1			
C. stevensi	C. inocephala	2	Calathea micans – CR	Heliconia sp. – CR	–
	C. latifolia	1			
	I. pruinosus	1			
C. suturalis	C. pulverulentus	1	Costus sp. – CR	–	–
C. trimaculata	C. pulverulentus	2	Renealmia sp. – PA	Costaceae – CR	–
C. sp61	B. major	1	–	–	–
	C. wendlandiana	1			
	O. panamanus	376			
Chelobasis bicolor	C. latifolia	1	–	Heliconia sp. – CR	H. curtispatha – CR
	H. catheta	1			H. imbricata – CR
	H. irrasa	1			**H. irrasa** – CR
	H. latispatha	10			**H. latispatha** – PA
	H. vaginalis	2			**H. latispatha** – CR
	H. wagneriana	1			Heliconia metallica – CR
					H. platystachys – PA
					H. wagneriana – CR
Chelobasis perplexa	H. irrasa	1	H. pogonantha – CR	C. insignis – CR	H. imbricata – CR
	H. mariae	23		H. imbricata – CR	H. latispatha – CR
Delocrania panamensis	B. major	1	–	–	–
	O. panamanus	20			
Homalispa nevermanni	O. panamanus	659	–	–	–
Imatidium thoracicum	C. lutea	3	–	Arecaceae – CR	–
	H. catheta	11		Zingiberales	
	H. irrasa	1		C. insignis – CR	
	H. latispatha	83			
	H. wagneriana	12			
Platocthispa emorsitans	C. insignis	8	–	Calathea sp.	–

Table 4. *Continued*

Hispine species	Host plant in present study	No.	McKenna[1]	Staines[2]	Strong[3]
	C. latifolia	17		*Costus* sp.	
	H. catheta	1			
	H. irrasa	11		Piperaceae	
	H. latispatha	221			
Prosopodonta dorsata	*C. wendlandiana*	170	–	Arecaceae	–
	Cryosophila warscewiczii	24			
	O. panamanus	287			
Spaethiella circumdata	*H. irrasa*	37	–	–	–
	H. latispatha	1			
	H. vaginalis	2			
Spaethiella marginata	*C. insignis*	19	–	–	–
	H. catheta	16			
	H. latispatha	159			
	H. mariae	9			
	H. wagneriana	1			
Spaethiella tristis	*B. major*	117	–	–	–
	C. simpliciflora	4			
	O. panamanus	122			
Spaethiella sp47	*C. simpliciflora*	20	–	–	–
Stilpnaspis panamensis	*C. wendlandiana*	180	–	–	–
	O. panamanus	83			

Country codes are: PA, Panama; CR, Costa Rica; CO, Colombia; EC, Ecuador; species in bold, species common to both this study and previous reports.
[1] McKenna and Farrel (2005, 2006).
[2] Staines (1996, 2002, 2006).
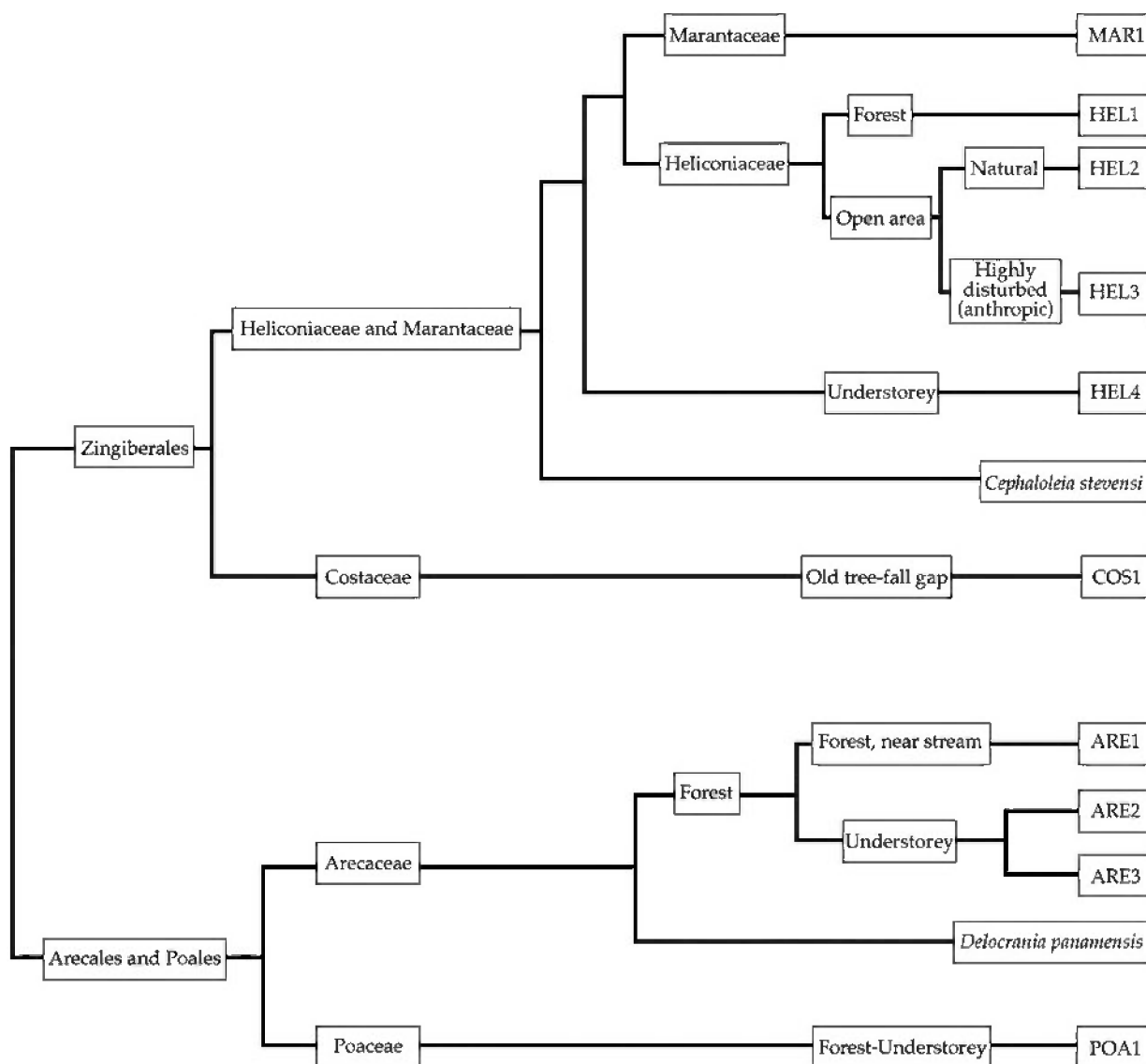[3] Strong (1977a,b, 1983); Strong *et al.* (1984).

Fig. 3. Synthesis of the relationships between plant family, habitat and hispoid Cassidinae assemblage composition based on cluster analysis results (average linkage method; Bray–Curtis' distance). ARE1, first cluster group of Arecaceae; ARE2, second cluster group of Arecaceae; ARE3, third cluster group of Arecaceae; HEL1, first cluster group of Heliconiaceae; HEL2, second cluster group of Heliconiaceae; HEL3, third cluster group of Heliconiaceae; HEL4, fourth cluster group of Heliconiaceae; COS1, cluster group of Costaceae; MAR1, cluster group of Marantaceae; POA1, cluster group of Poaceae

beetle assemblages (Tables 3 and 4). Table 3 clarifies the cluster nodes (Fig. 2) according to the host plant species' habitats. However, the fit of some hispine species into these nodes is not clear-cut. For example, *Aslamidium semicircularum*, an 'open-leaf scraper' species that seems to be a 'family specialist' (Barone, 1998; McKenna and Farrell, 2005, 2006), actually occurs on many Marantaceae species (Table 3). This species does not, to our knowledge, feed on other monocot families, including the Arecaceae as indicated by Staines (2002). Conversely, *Cephaloleia sallei* seems to be strongly specialized on

a single plant species: *C. latifolia*, much as *Homalispa nevermanni* occurs on only *Oenocarpus panamanus* among the four palm species we examined. If we follow the feeding concepts of Barone (1998), *C. sallei* and *H. nevermanni* could be termed as 'species specialists'. In our study areas, *C. sallei* is a feeding specialist on primarily one species of Zingiberales (Table 3), contrary to other accounts that suggest it is a generalist (McKenna and Farrell, 2005).

Taxonomy can complicate the comparison and interpretation of results from this study and previous studies. For example, the polymorphic

leaf miner, *Platocthispa emorsitans*, is intimately associated with *H. latispatha*, a common resident in shady anthropically disturbed areas such as roadsides and power transmission line cuts. However, this hispine was also occasionally reared from *Calathea insignis*, *C. latifolia* and *Heliconia irrasa*. Future genetic studies will be needed to test whether individuals reared from *Calathea* and *Heliconia* mines belong to the same or different species. An additional example is provided by *Cephaloleia vicina* Baly and *Cephaloleia belti* whose morphologies are extremely similar and occur on the same species of the Heliconiaceae in different areas. *Cephaloleia belti* occurred in this study primarily on the Heliconiaceae but also in smaller numbers on the Marantaceae. According to a preliminary molecular phylogenetic analysis (Descampe and Meskens unpublished data), the *C. belti* individuals collected in this study appear to belong to a single species.

Another taxonomic problem is presented by the genus *Nympharescus* Weise, which Strong (1982) records from the northern Panama Canal area, but both Blackwelder (1946) and Staines (2002) indicate it is absent from Central America but present from Colombia to Peru. It now appears that this species, which was recorded as a common resident in *Heliconia mariae* scrolls, is a morphological variant of *Chelobasis perplexa* which closely resembles some *Nympharescus* species.

Based on the occurrence data presented in this study and feeding trials (Descampe *et al.*, 2007, in press; Meskens unpublished data), we conclude that most hispines feed on more than one related plant species, often on several genera and families but rarely cross to feed on different orders of monocot plants. The feeding flexibility which we have documented is best exemplified by *C. belti* which occurred in the leaf scrolls of eight species, three genera and two families of Zingiberales.

Acknowledgements

References

Allaby M. (2003) *Oxford Dictionary of Zoology*. Oxford University Press, New York, NY. 597 pp.

Baly J. S. (1885–1894) *Biologica Centrali-Americana*. Insecta. Coleoptera, Vol. VI Part 2. Phytophaga (part). Hispidae. Taylor and Francis, London.

Barone J. A. (1998) Host-specificity of folivorous insects in a moist tropical forest. *Journal of Animal Ecology* 67, 400–409.

Berry F. and Kress W. J. (1991) *Heliconia: An Identification Guide*. Smithsonian Institution Press, London. 334 pp.

Blackwelder R. E. (1946) Checklist of the coleopterous insects of Mexico, Central America, The West Indies, and South America. *Smithsonian Institution United States National Museum Bulletin* 185, 551–764.

Chaboo C. (2007) Biology and phylogeny of the Cassidinae Gyllenhal sensu lato (tortoise and leaf-mining beetles) (Coleoptera: Chrysomelidae). *Bulletin of the American Museum of Natural History* 205, 1–250.

Chaboo C. and Nguyen T. C. (2004) Immatures of *Hemisphaerota palmarum* (Boheman), with discussion of the caudal processes and shield architecture in the tribe Hemisphaerotini (Chrysomelidae, Cassidinae), pp. 171–184. In *New Developments in the Biology of Chrysomelidae* (Edited by P. Jolivet, J. A. Santiago-Blay and M. Schmitt). SPB Academic Publishing BV., The Hague.

Chave J. (2004) Neutral theory and community ecology. *Ecology Letters* 7, 241–253.

Croat T. B. (1978) *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California. 943 pp.

Descampe A., Meskens C., Windsor D. M. and Hance T. (2007) From potential to realized niche: Feeding flexibility of Neotropical hispine beetles (Chrysomelidae: Cassidinae: Cephaloleiini) *Environmental Entomology* (in press).

Dobler S., Mardulyn P., Pasteels J. M. and Rowell-Rahier M. (1996) Host plant switches and the evolution of the chemical defence and life history in the leaf beetle genus *Oreina*. *Evolution* 50, 2373–2386.

Dufrêne M. and Legendre P. (1997) Species assemblages and species indicators: The need of a flexible asymmetrical approach. *Ecological Monographs* 67, 345–366.

Fernandez P. and Hilker M. (2007) Host plant location by Chrysomelidae. *Basic and Applied Ecology* 8, 97–116.

Flowers R. W. and Janzen D. H. (1997) Feeding records of Costa Rican leaf beetles (Coleoptera: Chrysomelidae). *Florida Entomologist* 80, 334–366.

Hespenheide D. H. and Dang V. (1999) Biology and ecology of leaf-mining Hispinae (Coleoptera, Chrysomelidae) of the La Selva Biological Station, Costa Rica, pp. 375–389. In *Advances in Chrysomelidae Biology 1* (Edited by M. L. Cox). Backhuys Publishers, Leiden, The Netherlands.

Hsiao T. H. and Windsor D. M. (1999) Historical and biological relationships among Hispinae inferred from 12S MTDNA sequence data, pp. 39–50. In

Advances in Chrysomelidae Biology 1 (Edited by M. L. Cox). Backhuys Publishers, Leiden.

Janssen T. and Bremer K. (2004) The age of major monocot groups inferred from 800 + *rbcL* sequences. *Botanical Journal of the Linnean Society* 146, 385–398.

Jolivet P. (1997) *Biologie des coléoptères chrysomélides*. Société nouvelle des éditions Boubée, Paris. 279 pp.

Kress W. J. (1990) The phylogeny and classification of the Zingiberales. *Annals of Missouri Botanical Garden* 77, 698–721.

Legendre P. and Legendre L. (1998) *Numerical Ecology*. Elsevier Inc., San Diego, California. 853 pp.

McKenna D. D. and Farrell B. D. (2005) Molecular phylogenetics and evolution of host plant use in the Neotropical rolled leaf 'hispine' beetle genus *Cephaloleia* (Chevrolat) (Chrysomelidae: Cassidinae). *Molecular Phylogenetics and Evolution* 37, 117–131.

McKenna D. D. and Farrell B. D. (2006) Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Procedings of the National Academy of Sciences*, USA 103, 10947–10951.

Novotny V., Basset Y., Miller S. E., Weiblen G. D., Bremer B., Cizek L. and Drozd P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature* 416, 841–844.

Pisces Conservation (2002a) Community Analysis Package, Version 2.0. Conservation Limited, Pennington, Lymington, Hants.

Pisces Conservation (2002b) Species Diversity and Richness, Version 3.0. Pisces Conservation Limited, Pennington, Lymington, Hants.

Seifert R. P. (1982) Neotropical *Heliconia* insect communities. *Quarterly Review of Biology* 57, 1–28.

Seifert R. P. and Seifert F. H. (1976) A community matrix of *Heliconia* insect communities. *American Naturalist* 110 (973), 461–483.

Soltis P., Endress P., Chase M. and Soltis D. (2005) *Phylogeny and Evolution of Angiosperms*. Sinauer Associates Inc., Sunderland, Massachusetts. 364 pp.

SPSS Inc. (2000) Systat, Version 10. SPSS Inc., Chicago, Illinois.

Staines C. L. (1996) The genus *Cephaloleia* (Coleoptera: Chrysomelidae) in Central America and the West Indies. *Revista de Biologia Tropical* 3, 3–87 Special Publication.

Staines C. L. (2002) The New World tribes and genera of hispines (Coleoptera: Chrysomelidae. Cassidinae). *Proceedings of the Entomological Society of Washington* 104 (3), 721–784.

Staines C. L. (2004) Cassidinae (Coleoptera, Chrysomelidae) and Zingiberales: A review of the literature, pp. 307–319. In *New Developments in the Biology of Chrysomelidae* (Edited by P. Jolivet, J. A. Santiago-Blay and M. Schmit). SPB Academic Publishing, The Hague.

Strong D. R. (1977a) Rolled-leaf hispine beetles (Chrysomelidae) and their Zingiberales host plants in Middle America. *Biotropica* 9, 156–169.

Strong D. R. (1977b) Insect species richness: Hispine beetles of *Heliconia latispatha*. *Ecology* 58, 573–582.

Strong D. R. (1982) Harmonious coexistence of hispine beetles on *Heliconia* in experimental and natural communities. *Ecology* 63, 1039–1049.

Strong D. R. (1983) *Chelobasis bicolor* (rolled-leaf hispine), pp. 708–711. In *Costa Rican Natural History* (Edited by D. H. Janzen). The University of Chicago Press, Chicago, Illinois.

Strong D. R., Lawton J. H. and Southwood T. (1984) *Insects on Plants: Community Patterns and Mechanisms*. Harvard University Press, Cambridge, Massachusetts. 313 pp.

Wilf P., Labandeira C. C., Kress W. J., Staines C. L., Windsor D. M., Allen A. L. and Johnson K. R. (2000) Timing the radiations of leaf beetles: Hispines on gingers from latest Cretaceous to recent. *Science* 289, 291–294.

Williams C. A. and Harborne J. B. (1977) The leaf flavonoids of the Zingiberales. *Biochemical Systematics and Ecology* 5, 221–229.