

Floral associations of cyclocephaline scarab beetles

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Abstract

The scarab beetle tribe Cyclocephalini (Coleoptera: Scarabaeidae: Dynastinae) is the second largest tribe of rhinoceros beetles, with nearly 500 described species. This diverse group is most closely associated with early diverging angiosperm groups (the family Nymphaeaceae, magnoliid clade, and monocots), where they feed, mate, and receive the benefit of thermal rewards from the host plant. Cyclocephaline floral association data have never been synthesized, and a comprehensive review of this ecological interaction was necessary to promote research by updating nomenclature, identifying inconsistencies in the data, and reporting previously unpublished data. Based on the most specific data, at least 97 cyclocephaline beetle species have been reported from the flowers of 58 plant genera representing 17 families and 15 orders. Thirteen new cyclocephaline floral associations are reported herein. Six cyclocephaline and 25 plant synonyms were reported in the literature and on beetle voucher specimen labels, and these were updated to reflect current nomenclature. The valid names of three unavailable plant host names were identified. We review the cyclocephaline floral associations with respect to inferred relationships of angiosperm orders. Ten genera of cyclocephaline beetles have been recorded from flowers of early diverging angiosperm groups. In contrast, only one genus, Cyclocephala, has been recorded from dicot flowers. Cyclocephaline visitation of dicot flowers is limited to the New World, and it is unknown whether this is evolutionary meaningful or the result of sampling bias and incomplete data. The most important areas for future research include: 1) elucidating the factors that attract cyclocephalines to flowers including floral scent chemistry and thermogenesis, 2) determining whether cyclocephaline dicot visitation is truly limited to the New World, and 3) inferring evolutionary relationships within the Cyclocephalini to rigorously test vicarance hypotheses, host plant shifts, and mutualisms with angiosperms.

Keywords: Cantharophily, Scarabaeidae, Dynastinae, Araceae, Arecaceae, Annonaceae, Nymphaceae

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Introduction

The Cyclocephalini (Coleoptera: Scarabaeidae: Dynastinae) is the second largest rhinoceros beetle tribe, currently containing 15 genera and nearly 500 described beetle species (Jameson et al. 2002; Ratcliffe 2003; Smith 2006). Cyclocephalines have a pantropical distribution, though the majority of the group's generic and species diversity is concentrated in the New World (Ratcliffe 2003; Ratcliffe and Cave 2006). Most genera are sexually dimorphic, with males having enlarged protarsal claws and females having expanded elytral epipleura (Moore 2012). Cyclocephalines are important economically and ecologically as root pests (larvae) and pollinators (adults) (Ratcliffe 2003; Ratcliffe and Paulsen 2008). Adult cyclocephaline beetles can be found within the inflorescences of early diverging angiosperm groups (the family Nymphaeaceae, magnoliid clade, and monocots; Figure 1) and have been shown to contribute to pollination in the Annonaceae, Araceae, Arecaceae, Cyclanthaceae, Magnoliaceae, and Nymphaeaceae (Cramer et al. 1975; Beach 1982; Beach 1984; Young 1986; Young 1988b; Gottsberger 1989; Dieringer et al. 1999; Hirthe and Porembski 2003; Maia et al. 2012). Studies of these interactions indicate that some early diverging angiosperm groups offer rewards to cyclocephalines in the form of mating sites, food, and metabolic boosts associated with floral thermogenicity in return for pollination services (Gottsberger 1986; Young 1986; Seymour et al. 2009). Cyclocephaline visitation of dicot flowers is poorly known and little studied.

Cyclocephaline floral associations have been reported in journals, books, and monographs since the late 18th century. However, the prevalence, geographic scope, and biological importance of these records are difficult to gauge because publications summarizing cyclocephaline floral visitation are somewhat dated and report floral visitation only for specific plant families, geographic areas, or vegetation types (Henderson 1986; Gibernau 2003; Gottsberger and Silberbauer-Gottsberger 2006; Gibernau 2011). The fragmentary nature of these data and the citation of unpublished observations have hampered the ability to identify floral association trends within cyclocephaline genera and species.

The phylogeny of the Cyclocephalini was investigated for the first time by Clark (2011), and the generic-level relationships within the tribe remain an area of active research by M. R. Moore. Tribal circumscription of the Cyclocephalini is subject to change based on ongoing phylogenetic analyses. This research will provide an evolutionary framework for interpreting patterns of floral visitation. Compilation and synthesis of a checklist of floral associations is needed in order to understand the ecology of the Cyclocephalini within a phylogenetic context.

This checklist synthesizes data (plant and beetle species, geographic locality, and original citation) for the floral associations of adult cyclocephaline beetles. Invalid nomenclature in the surveyed literature is identified and corrected; conflicting data, sources of error, and uncertainty in the data are identified; and unpublished floral association data from examined voucher specimens are added. The aim of this work is to promote future research of these ecological interactions by providing a comprehensive data set of the taxonomic and geographic scope of floral visitation for cyclocephaline beetles.

Materials and Methods

Literature was surveyed from 1758 (Linnaeus) to 2012. Keyword searches for all cyclocephaline genera (sensu Ratcliffe and Cave 2006; Clark 2011) were conducted in the following databases: BioOne® (www.bioone.org), BIOSIS Previews® (http://apps.webofknowledge.com/), JSTOR (www.jstor.org), and Biodiversity Heritage Library (www.biodiversitylibrary.org). Every host plant reference from Pike et al. (1976) was checked for floral association data.

All reported cyclocephaline species names from the literature were verified by referencing the original species description and monographic treatments of the Dynastinae (Endrödi 1985; Ratcliffe 2003; Ratcliffe and Cave 2006). Synonyms or misspelled cyclocephaline species names in the literature were updated to reflect current nomenclature. All reported host plant names were verified using the peer-reviewed botanical taxonomic databases Tropicos (www.tropicos.org) and The Plant List (www.plantlist.org). Synonyms or misspelled plant names were updated to reflect current nomenclature based on The Plant List (2010). In some cases, scientific names in the literature could not be identified as valid or invalid (e.g., unavailable manuscript names or conflicting synonyms). Some unverified plant names were reported according to the original citation for the floral association, and the name was noted as unresolved. Occasionally, host plant and beetle species were not assigned an author in the reference for an association. This caused problems due to the prevalence of synonyms and homonyms in the plant and insect literature. Resulting ambiguities were rectified to the extent possible and explained in the remarks column (Appendix 1).

Borrowed specimens of cyclocephaline species allowed for direct evaluation of specieslevel identifications that were reported by several authors. Particularly, this included of Cyclocephala sexpunctata Laporte (1840) and C. brevis Höhne (1847) collected by George Schatz, Helen Young (La Selva Biological Station, Costa Rica), Alberto Seres, and Nelson Ramirez (Henri Pittier National Park, Venezuela), with association data that were subsequently published or unpublished. Identifications of these specimens (or specimen vouchers) were critically examined (Moore 2011). Exemplar material borrowed from the University of Ne-Museum (authoritatively braska State identified by B. C. Ratcliffe) and monographic treatments (Ratcliffe 2003; Ratcliffe and Cave 2006) served as the basis for evaluating species identifications as well as detailed images of some type specimens. The operating assumption was that the collectors and authors were consistent with their species-level determinations. Identifications deemed incorrect based on current taxonomy were updated and noted accordingly. Unpublished host plant data were also found with cyclocephaline specimens in collections. These specimens were collected by M. R. Moore and deposited at Wichita State University, Wichita, Kansas, USA, or loaned from the following institutions:

INBC: Instituto Nacional de Biodiversidad, Santo Domingo de Herédia, Costa Rica (Angel Solís)

MLUH: Zentralmagazin Naturwissenschaftlicher Sammlungen, Martin Luther Universität Halle-Wittenberg, Halle, Saxony-Anhalt, Germany (Karla Schneider)

MNHN: Muséum national d'Histoire naturelle, Paris, France (Olivier Montreuil)

SEMC: Snow Entomological Museum, University of Kansas, Lawrence, KS (Zach Falin and Jennifer Thomas)

UNSM: University of Nebraska State Museum, Lincoln, NE (Brett Ratcliffe and Matt Paulsen)

USNM: U.S. National Museum, Washington, D.C. (currently housed at the University of Nebraska State Museum for off-site enhancement) (Floyd Shockley and Dave Furth)

UVGC: Universidad del Valle de Guatemala, Guatemala City, Guatemala (Jack Schuster and Enio Cano)

WICH: Wichita State University, Wichita, KS (Mary Liz Jameson)

ZMHB: Museum für Naturkunde der Humboldt Universität zu Berlin, Berlin, Germany (Johannes Frisch and Joachim Willers)

Concrete and anecdotal evidence of floral associations were also included in the checklist. The nature of the published association occasionally needed clarification or elaboration (e.g., cyclocephalines reported near flowers but not on them or museum specimens covered in resin and pollen). These clarifications were provided in the remarks column of Appendix 1. A large amount of unpublished and inaccessible data exists with regard to cyclocephaline floral visitation. These records provide ambiguous data for plant species, cyclocephaline species, locality, and associated voucher information. For example, Schatz (1990, Table 7.3) recorded known and predicted (without distinguishing the two) plant taxa pollinated by dynastines in the Neotropics. Schatz (1990, Table 7.4) recorded cyclocephaline plant visitation at La Selva Biological Station, but a large amount of data could not be extracted because of the nonspecific nature of the record (i.e., the data were reported at the tribal-level rather than at the species-level). These inaccessible data are important because they report certain associations that are not recorded elsewhere in the literature. Repetitive data from these types of records were omitted from the checklist. Only unique generic or species-level plant associa-

Scarab Taxa	Plant Taxa	Locality	Collector	Depository
Cyclocephala atripes Bates, 1888	Dieffenbachia tonduzii Croat & Grayum	COSTA RICA: Herédia (La Selva Biol. Stat.)	M. Grayum	3 vouchers in INBC
Cyclocephala brevis Höhne, 1847 incertae cedis	Dieffenbachia seguine (Jacq.) Schott	VENEZUELA: Aragua (Henri Pittier National Park)	A. Seres and N. Ramirez	1 voucher in USNM
(Cyclocephala morphospecies 3 sensu Moore 2011)	Philodendron ligulatum Schott	COSTA RICA: Herédia (La Selva Biol. Stat.)	H. Young	1 voucher in INBC
Cyclocephala brevis Höhne, 1847 incertae cedis (Cyclocephala morphospecies 4 sensu Moore 2011)	Philodendron sp.	PANAMA: Colón (1 km E Rio Guanche Bridge)	B. Ratcliffe and M. Jameson	1 voucher in UNSM
Cyclocephala octopunctata Burmeister, 1847	Annona dioica A. St Hil.	BOLIVIA: Santa Cruz uncredited		1 voucher in UNSM
Cyclocephala ovulum Bates, 1888	Inga sp.	ECUADOR: Napo (Yasuni Research Station)	M. Jameson	1 plant voucher in WICH
Cuele combale meeting (Olivier, 1790)	Arecaceae	BRAZIL: Manaus (Reserva Ducke)	S. Vidal	2 vouchers in UNSM
Cyclocephala rustica (Olivier, 1789)	Dieffenbachia seguine (Jacq.) Schott	FRENCH GUIANA: Dept 973 (Nouragues)	M. Gibernau	5 vouchers in UNSM
Cyclocephala santaritae Ratcliffe, 1992a	Oenocarpus sp.	ECUADOR: Napo	H. Balslev and A. Henderson	3 vouchers in UNSM
Cyclocephala sexpunctata Laporte, 1840 incertae sedis (Cyclocephala morphospecies 2 sensu Moore 2011)	Alocasia macrorrhizos (L.) G. Don	COSTA RICA: San José (Parque del Este)	Uncredited (likely collected by C. Valerio, see Valerio 1984)	8 vouchers in UNSM
Cyclocephala undata (Olivier, 1789)	Duguetia asterotricha (Diels) R. E. Fr.	BRAZIL: Manaus	G. Gottsberger	1 voucher in UNSM
Erioscelis proba Sharp, 1877	Dieffenbachia seguine (Jacq.) Schott	FRENCH GUIANA (Nouragues Field Station)	M. Gibernau	28 vouchers in UNSM
Mimeoma signatoides (Höhne, 1923)	Socratea sp.	VENEZUELA (Henri Pittier National Park)	A. Seres and N. Ramirez	1 voucher in USNM

tions were reported for the beetle tribe from these data sets. These non-specific records are reported at the end the checklist with the intention that they be reevaluated with the addition of more data.

Results

Based on species-specific records from the literature and voucher label data, at least 97 cyclocephaline species from nine or 10 genera (depending on the identity of the cyclocephaline reported by Gibbs et al. (1977)) were recorded in association with the flowers of at least 161 species representing 58 genera, 17 families, and 15 orders (Appendix 1). Examined voucher specimens occasionally had unique, unpublished, floral association data. Thirteen new plant associations are provided in Table 1. Examined voucher specimens that did not have unique data are noted in Appendix 1. The most specific data are summarized at the generic-level for the plant association (plant classification according to the Angiosperm Phylogeny Group III (2009)) in Table 2 and are provided in full detail (lowest-level taxonomy, geographic data, and references) in Appendix 1. Cyclocephaline beetle genera and their associations with angiosperm plant lineages were mapped onto the APG III angiosperm phylogeny (Figure 1).

Five of the 15 cyclocephaline genera were not reported as floral visitors in any of the surveyed literature: *Acrobolbia* Ohaus (1912), *Ancognatha* Erichson (1847), *Harposcelis* Burmeister (1847), *Stenocrates* Burmeister (1847), and *Surutu* Martínez (1955). Preliminary phylogenetic analysis of the Cyclocephalini indicated that the Neotropical genus *Parapucaya* Prell (1934) (Dynastinae: Pentodontini) and the Indonesian archipelago genus *Neohyphus* Heller (1896) (Dynastinae: Oryctoderini) fall within a potential newly

Table 2. Generic-level summary of floral association records for the Cyclocephalini (group names in parentheses are based on APG III (2009)) [? indicates a potentially dubius record, see Appendix I].

Plant Taxa	Scarab Genera
	HAELES
	haeaceae
100 000	Cyclocephala Dejean
Nymphaea	Ruteloryctes Arrow
	Arriguttia Martinez
Victoria	Chalepides Casey
riciona	Cyclocephala
MACN	OLIALES
A CONTRACT OF A	onaceae
Ailiit	Cyclocephala
Annona	Dyscinetus Harold (?)
Contraction	
Cymbopetalum	Cyclocephala
Duguetia	Cyclocephala
Malmea	Cyclocephala
Porcelia	Cyclocephala
Magn	oliaceae
Magnolia	Augoderia Burmeister (
magnoma	Cyclocephala
ALISM	IATALES
Ar	aceae
Alocasia	Cyclocephala
Amorphophallus	Peltonotus Burmeiste
Caladium	Cyclocephala
Colocasia	Cyclocephala
	Cyclocephala
Dieffenbachia	Erioscelis Burmeiste
Epipremnum	Peltonotus
Gearum	Cyclocephala
Monstera	Cyclocephala
	Aspidolea Bates
Montrichardia	Cyclocephala
Monthienaraia	Erioscelis
	Cyclocephala
Philodendron	Erioscelis
Rhodospatha	Cyclocephala
Knouospuina	
Syngonium	Cyclocephala
The control	Erioscelis
Taccarum	Cyclocephala
V	Cyclocephala
Xanthosoma	
	Erioscelis
Araceae undetermined	Erioscelis Arriguttia Martínez
Araceae undetermined PAND	Erioscelis Arriguttia Martínez ANALES
Araceae undetermined PAND Cycla	Erioscelis Arriguttia Martínez ANALES nthaceae
Araceae undetermined PANDA Cyclai Asplundia	Erioscelis Arriguttia Martínez ANALES nthaceae Cyclocephala
Araceae undetermined PANDA Cyclai Asplundia Carludovica	Erioscelis Arriguttia Martínez ANALES nthaceae
Araceae undetermined PANDA Cyclai Asplundia	Erioscelis Arriguttia Martínez ANALES nthaceae Cyclocephala
Araceae undetermined PAND Cyclai Asplundia Carludovica Cyclanthus	Erioscelis Arriguttia Martínez ANALES nthaceae Cyclocephala Cyclocephala
Araceae undetermined PAND Cyclar Asplundia Carludovica Cyclanthus ARE	Erioscelis Arriguttia Martínez ANALES nthaceae Cyclocephala Cyclocephala Cyclocephala
Araceae undetermined PAND Cyclar Asplundia Carludovica Cyclanthus ARE	Erioscelis Arriguttia Martínez ANALES nthaceae Cyclocephala Cyclocephala Cyclocephala Cyclocephala CALES
Araceae undetermined PAND Cyclai Asplundia Carludovica Cyclanthus ARE Acrocomia	Erioscelis Arriguttia Martínez ANALES nthaceae
Araceae undetermined PAND Cyclar Asplundia Carludovica Cyclanthus ARE Acrocomia Aphandra	Erioscelis Arriguttia Martínez ANALES nthaceae
Araceae undetermined PAND Cyclai Asplundia Carludovica Cyclanthus ARE Acrocomia	Erioscelis Arriguttia Martínez ANALES nthaceae Cyclocephala Cyclocephala Cyclocephala CALES caceae Cyclocephala Cyclocephala Cyclocephala Cyclocephala
Araceae undetermined PAND Cyclai Asplundia Carludovica Cyclanthus ARE Acrocomia Aphandra Astrocaryum	Erioscelis Arriguttia Martínez ANALES nthaceae Cyclocephala Cyclocephala Cyclocephala CALES caceae Cyclocephala Cyclocephala Cyclocephala Cyclocephala Mimeoma Casey
Araceae undetermined PAND Cyclar Asplundia Carludovica Cyclanthus ARE Acrocomia Aphandra	Erioscelis Arriguttia Martínez ANALES nthaceae Cyclocephala Mimeoma Casey Cyclocephala
Araceae undetermined PAND Cyclai Asplundia Carludovica Cyclanthus ARE Acrocomia Aphandra Astrocaryum	Erioscelis Arriguttia Martínez ANALES nthaceae Cyclocephala Mimeoma Casey Cyclocephala Cyclocephala
Araceae undetermined PAND Cyclai Asplundia Carludovica Cyclanthus ARE Acrocomia Aphandra Astrocaryum Attalea	Erioscelis Arriguttia Martínez ANALES nthaceae Cyclocephala Mimeoma Casey Cyclocephala

	Aspidolea
Oenocarpus –	Cyclocephala
Phytelephas	Cyclocephala
	Cyclocephala
Socratea	Mimeoma
Syagrus	Cyclocephala
Wettinia	Cyclocephala
FABA	LES
Faba	ceae
Acacia	Cyclocephala
Pithecellobium	Cyclocephala
Inga	Cyclocephala
ROSA	LES
Mora	ceae
Ficus	Cyclocephala
MALPIG	HIALES
Calophy	llaceae
Kielmeyera	Cyclocephala
MYRT	ALES
Myrta	aceae
Psidium	Cyclocephala
MALV	ALES
Malva	
Hibiscus	Cyclocephala
CARYOPH	
Cacta	OFFICE AND ADDRESS OF THE PARTY
Cereus	Cyclocephala
Echinopsis	Cyclocephala
Opuntia	Cyclocephala
ERICA	
Lecythi	
Corythophora	Cyclocephala
Eschweilera	Cyclocephala
Lecythis	Cyclocephala
Sapot	
Pouteria	Cyclocephala
ASTER	BEAUTION OF THE STREET
Verbesina	Cyclocephala Cyclocephala
SOLAN	
Solan	
Brugmansia	Cyclocephala
Datura	Cyclocephala
GENTIA	
Apocyi	
Apocyi	THE PARTY OF THE P
Hancornia	
Hancornia Mandevilla	Cyclocephala Cyclocephala

defined Cyclocephalini (Clark 2011). These genera were included in the systematic literature searches but yielded no floral association records. The results of Clark (2011) hypothesized that the genus *Erioscelis* Burmeister

(1847) is sister to all remaining genera of the Cyclocephalini + *Neohyphyus* + *Parapucaya*. *Erioscelis* was included in this checklist because of its documented visitation of several genera in the Araceae (also visited by other cyclocephalines) and its historical inclusion in the Cyclocephalini.

Floral associations that are less specific or ambiguous (non-specific records) were also reported (Appendix 1). For example, Listabarth (1996) reported dynastine scarabs, with no further species identification, on three species of *Bactris* palms (Arecales). These data include records for Scarabaeidae, Dynastinae, and beetles on flowers that fit the general pattern of cyclocephaline floral visitation (nocturnal visitation of bowl-shaped, thermogenic inflorescences). Non-specific records were included in the checklist with the hope that they may be reevaluated with additional data.

Gathering and interpreting floral association data were complicated by the prevalancy of synonyms, invalid names, and unavailable names in the literature. Based on The International Code of Zoological Nomenclature (ICZN 1999), an unavailable name is a name that is excluded from use due to the requirements of the code. For example, the unavailable name Cyclocephala inpunctata was reported in the surveyed literature (Gottsberger 1986, 1988). C. inpunctata has never been described in the literature. This name is unavailable and was likely reported in error. Based on published locality data for the floral association, images of the beetle (Gottsberger 1988; Figure 4a, 5 a-d), and subsequently published records, we consider this species to be Cyclocephala quatuordecimpunctata Mannerheim (1829) (personal communication with B. C. Ratcliffe, April 2011). Synonyms of six cyclocephaline genus or species names were reported in the surveyed literature; these invalid names were updated based on current nomenclature (Appendix 2). Synonyms of 25 plant genus or species names were reported in the surveyed literature and on voucher specimen label data; these invalid names were updated based on current nomenclature (Appendix 3).

Seven unresolved or unavailable plant names were reported from label data and in the surveyed literature (Appendix 4). According to The Plant List (2010), unresolved names are those for which "it is not yet possible to assign a status of either 'accepted' or 'synonym." Two of these names, Philodendron atlanticum and Dieffenbachia longivaginata, were unavailable manuscript names (place-holder names for species that were later described) of Thomas Croat and Michael Grayum (Missouri Botanical Garden, St. Louis, Missouri, USA). These species were identified as *Philodendron* ligulatum Schott and Dieffenbachia tonduzii Croat and Grayum, respectively (personal communication with T. Croat and M. Grayum, April 2011). Xanthosoma macrorrhizas is an unavailable name that was reported by Valerio (1984). This species may be the cultivated, naturalized, non-native species Alocasia macrorrhizos (L.) G. Don (personal communication with T. Croat, April 2011).

Certain cyclocephaline species were commonly reported as floral visitors. For example, *Cyclocephala sexpunctata* had over 20 floral visitation records in the surveyed literature (Appendix 1). *C. sexpunctata* is externally nearly identical to *C. brevis* (*sensu* Ratcliffe 2003; Ratcliffe and Cave 2006). Research on these two species showed that they represent four, or potentially five, morphospecies (Moore 2011). This conclusion was based on male genitalic characters, the form of the female epipleuron, and extensive range and

spatial data (Moore 2011). The taxonomy of the species *C. sexpunctata* and *C. brevis* remains unresolved (a possible species complex), and their floral associations were reported in detail (Moore 2011). Some voucher specimens for reported floral associations of *C. sexpunctata* and *C. brevis* remain to be examined, and some data will require reinterpretation after the examination of type specimens.

Discussion

Examination of cyclocephaline floral associations with respect to inferred relationships of angiosperm orders revealed that 10 of the 15 genera of cyclocephaline beetles have been recorded from flowers of early diverging angiosperm groups (the family Nymphaeaceae, magnoliid clade, and monocots; Figure 1). In contrast, only one genus, Cyclocephala, has been recorded from dicot flowers (Figure 1). Experimental and observational studies have demonstrated that cyclocephalines can act as pollinators in Nymphaeales, Magnoliales, Arecales, Pandanales, and Alismatales (Figure 1; Table 2) (Cramer et al. 1975; Beach 1982; Beach 1984; Young 1986; Young 1988b; Gottsberger 1989; Dieringer et al. 1999; Hirthe and Porembski 2003; Maia et al. 2012). In these early diverging plant groups, a wide set of floral traits and floral pollination syndromes indicate a correlation cyclocephaline beetles (large pollen grains with sticky exudates, sturdy and funnelshaped inflorescences or large disc-shaped flowers, timing of anthesis, and thermogenesis) (Thien et al. 2009; Gibernau et al. 2010). These angiosperm orders offer rewards to cvclocephalines in the form of mating sites, food, and heat resources associated with floral thermogenicity (Young 1986; Seymour et al. 2009).

Some cyclocephaline/flower associations are mutualistic (Cramer et al. 1975; Beach 1982; Beach 1984; Young 1986; Young 1988b; Gottsberger 1989; Dieringer et al. 1999; Hirthe and Porembski 2003; Maia et al. 2012). Ervik and Knudsen (2003) provide a compelling argument that scarab pollination of the Nymphaeaceae (Nymphales) is a mutualistic relationship that dates to the early Cretaceous. Whether this represents an example of coevolution is unclear, and only one study has addressed this hypothesis (Schiestl and Dötterl 2012). Schiestl and Dötterl (2012) argued that volatile organic compound production/detection arose in systems the Scarabaeoidea during the Jurassic, whereas floral volatile organic compounds arose in the Cretaceous/Paleocene. This was taken as evidence that early diverging angiosperm plant/scarab associations evolved due to a preexisting sensory bias in scarabs rather than as a result of coevolution (Schiestl and Dötterl 2012). However, coevolution could not be ruled out for the mutualism between cyclocephaline scarabs and aroid flowers (Schiestl and Dötterl 2012).

Floral visitation of the core eudicot clade (Figure 1) by cyclocephalines is poorly described and, in certain cases, significantly from a pollination mutualism. Such cases involve feeding and mating within flowers in which cyclocephalines have no apparent pollinating function and may destroy the reproductive capability of the plant. For example, in the Brazilian dicot Opuntia monocantha Haw. (Caryophyllales), Cyclocephala have been observed mating within the flowers and feeding on stamens (Lenzi and Inácio Orth 2011). Observations made on Echinopsis ancistrophora Speg. subsp. ancistrophora (Caryophyllales) flowers indicate that Cyclocephala visitors display destructive feeding behavior and do not contribute to reproduction (Schlumpberger et al. 2009). *Cyclocephala metrica* Steinheil (1874) was observed feeding on seeds in flower heads of *Verbesina encelioides* (Cav.) Benth. and Hook. f. ex A. Gray (Asterales) in Argentina (Hayward 1946). Seed predation in phytophagous scarabs is rare, the only other known example being some members of the subtribe Anisopliina (Scarabaeidae: Rutelinae: Anomalini) that feed on grass seeds (Poaceae) (Jameson et al. 2007).

In contrast to apparent destructive associations with dicots, only one detailed account provides evidence of a cyclocephaline beetle pollinating a eudicot. Prance (1976) observed male and female Cyclocephala verticalis Burmeister (1847) occupying the inflorescences of Lecythis, Corythophora, Eschweilera (Ericales) in Amazonas, Brazil. C. verticalis was strong enough to lift the closed androphore flap of Lecythidaceae (Ericales) inflorescences and displayed selective feeding of floral parts, eating only staminode tissue at the apex of the androphore and leaving fertile stamens untouched (Prance 1976). Based on these observations, C. verticalis was considered a likely pollinator of some Lecythidaceae genera, though this hypothesis was not tested (Prance 1976).

Gottsberger (1986) considered cyclocephaline floral visitation of the dicot families Apocynaceae (Gentianales), Calophyllaceae (Malpighiales), and Sapotaceae (Ericales) to be opportunistic. In the absence of early diverging angiosperm host flowers, Gottsberger (1986) hypothesized that cyclocephalines would visit strongly scented flowers of other groups. Cyclocephalines have been shown to aggregate based on floral scent compounds alone (Gottsberger et al. 2012). Cyclocephaline species (and populations) likely are biased towards a wide range of floral scent

compounds. Eudicot species with geographically variable floral scent profiles may evolve scents that incidentally stimulate cyclocephaline aggregation by randomly sampling the sensory bias range of scarabs present in that area (e.g., Schlumpberger and Raguso 2008; Schlumpberger et al. 2009). This scenario, if accurate, would lend support to the hypothesis of Schiestl and Dötterl (2012) that preexisting sensory biases in cyclocephalines have an important role in determining the host flower profile of a given cyclocephaline species.

Based on the assembled data (Appendix 1), cyclocephaline visitation of eudicots is limited to the New World. It is unknown whether this shift represents an evolutionary event that occurred in New World cyclocephalines. Observations of cyclocephalines on dicot flowers (Figure 1) have largely been made by chance and have not been the subject of rigorous experimentation or sampling protocols. Thus, it is quite possible that Old World cyclocephalines (Ruteloryctes, Peltonotus, and potentially *Neohyphus*) visit both early diverging angiosperm groups and dicot groups, but dicot associations have not been recorded. However, it is certain that the known diversity of host flowers lineages is much higher for New World cyclocephalines (15 orders, 17 families, and 58 genera) compared to Old World cyclocephalines (two orders, two families, and three genera) (Appendix 1). This correlation may indicate that the radiation of the cyclocephalines in the New World was accompanied by a subsequent increase in the diversity of their floral associations.

Cyclocephaline species are generally oligophagous or polyphagous. For cyclocephaline species with multiple host records, only seven species have been recorded from a single host plant genus (monophagous), 23 species have been reported from

multiple host plant genera within a family (oligophagous), and 27 species have been recorded from multiple host plant families (polyphagous) (Appendix 1). Single inflorescences often contain multiple cyclocephaline species, and an extreme example is Dieffenbachia nitidipetiolata Croat and Grayum (Alismatales), which was visited by at least nine Cyclocephala species at La Selva Biological Station, Costa Rica (Young 1990; see Croat 2004 for plant identification). These multi-species aggregations might be explained if floral scents are serving as sex pheromones for multiple cyclocephaline species (Schatz 1990). This hypothesis may be supported by the observations of Gottsberger et al. (2012) that Cyclocephala literata Burmeister will aggregate due to floral scent compounds alone.

The consequences of polyphagous and oligophagous cyclocephalines for pollination efficiency have been experimentally addressed, indicating that cyclocephaline floral visitors are differentially important as pollinators due to an interaction between their relative abundance and specific behavior (Young 1986, 1988a, b, 1990). It is less clear how cyclocephalines species, which often mate inside inflorescences, maintain sexual isolation in close proximity to multiple congenerics. A single infloresence may host large crowds of beetles, often more then 30 individuals (Maia et al. 2012). Sexual isolation may be maintained due to interspecific mating morphology (Moore 2012). Sexually dimorphic cyclocephaline species have enlarged protarsal claws (males), and the elytral epipleuron variably expanded into a shelf or flange (females). Morphological differences among epipleural expansions are useful for species-level identification in the Cyclocephalini (Ratcliffe 2003). Females have sclerotized patches, sometimes with setae, on the ventral portion of epipleural expansions (Moore

2012). It is hypothesized that the interaction between the male protarsal claw, the female epipleural expansions, and the ventral portion of the female elytra serves as a pre-copulatory sexual isolation mechanism. Further sexual isolation between species is accomplished by species-specific differences in male genitalic structure (Moore 2012). The male protarsal claw and the female epipleuron may also be involved in intraspecific mate competition. For example, male Cyclocephala gravis Bates were observed clinging tightly to the epipleural structures of a female (guarding behavior), thus limiting the mating access of other C. gravis males (Moore 2012). Cyclocephaline beetles exhibit some similarity to hopliine scarabs (Scarabaeidae: Rutelinae: Hopliini), which are generalist flower visitors in South Africa (Ahrens et al. 2011). Sexual dimorphism has evolved independently several times within the Hopliini (Ahrens et al. 2011). Evolution of sexual dimorphism in hopliines could be tied to the group's biology, as they feed and compete for mates within inflorescences (Midgeley 1992; Ahrens et al. 2011). Sexual dimorphism in cyclocephalines and hopliines may be analogous, driven by selection pressures related to oligophagous and polyphagous flower feeding, mating behavior, and host visitation.

Cyclocephaline beetles and floral associations provide an ideal system for investigating ecology (pollination, competition) and evolution (sexual selection, mutualisms). A well-founded phylogenetic framework for the Cyclocephalini is needed to advance this work. While ecological associations between beetles and early diverging angiosperm groups is fairly well-established, additional research is necessary to understand the ecological and historical associations of cyclocephaline beetles and dicots. Specifically, research is needed to address the apparent cyclocephaline

diversification on New World dicots. Research on cryptic species of host plants and beetles is fundamental to understanding this system. This includes the role of floral volatile compounds in attracting cyclocephaline beetles and patterns of pollination, herbivory, and interspecific competition within floral hosts.

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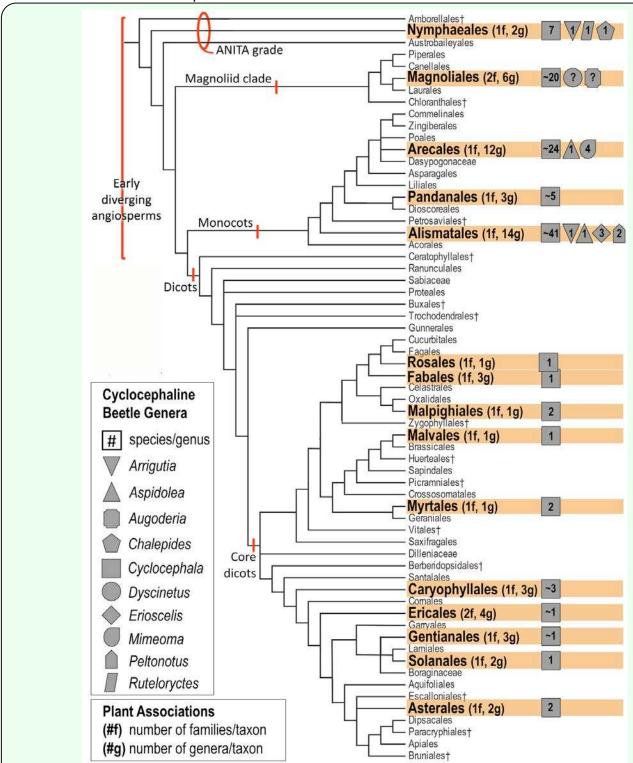


Figure 1. Cyclocephaline beetle genera and their associations with angiosperm plant lineages (plant phylogeny from APGIII 2009). Icons denote beetle genera that are associated with angiosperm plant lineages. Numbers in the icons indicate the number of species for each beetle genus. If the number of beetle species is unresolved due to conflict in the literature, this is indicated with \sim symbol (the number may be $\times \pm 1$ species). If the beetle genus has not been satisfactorily associated with the plant lineage, it is denoted with a ? symbol. For each angiosperm plant lineage, the number of families and genera that the beetles are associated with is denoted with #f (number of families) and #g (number of genera). See Appendix 1 for data. High quality figures are available online.

Appendix 1. Checklist of floral associations for the Cyclocephalini (Scarabaeidae: Dynastinae).

Beetle Taxon	Plant Taxon	Geographic Locality	References	Remarks
Arriguttia brevissima	Araceae	FRENCH GUIANA	Ponchel 2006	1 mm
(Апом, 1911)	Victoria amazonica (Poepp.) J. C. Sowerby	BRAZIL: Pará	Martinez 1968	<u> </u>
Aspidolea fuliginea Burmeister, 1847	Oenocarpus bataua Mart.	COLOMBIA: Antioquia, Chocó, Meta	Nunez-Avellaneda and Rojas-Robles 2008	-
Aspidolea quadrata Endrödi, 1980	Montrichardia arborescens (L.) Schott	FRENCH GUIANA: Kourou, Sinnamary	Gibernau et al. 2003; Ponchel 2006	æ
Augoderia nitidula Burmeister, 1847 or Cyclocephala nr. emarginata Endrödi, 1966 or Cyclocephala literata Burmeister, 1847	Magnolia ovata (A. St Hil.) Spreng.	BRAZIL: Minas Gerais, São Paulo	Gibbs et al. 1977	Gibbs et al. (1977) stated that the scarab was A. nitidula, but the figure legend reported the scarab species at Cyclocephala nr. emarginata Endröd 1966. Gottsberger (1986) reported the scarab species as C. literata.
Chalepides dilatatus (Mannerheim, 1829)	NO DATA	BRAZIL	Mannerheim 1829	177
Chalepides sp.	Victoria cruziana A. D. Orb.	ARGENTINA: Corrientes	Valla and Cirino 1972	
Cyclocephala abrelata Ratcliffe and Cave, 2002	NO DATA	HONDURAS: Yoro (Parque Nacional Pico Bonito)	Ratcliffe and Cave 2002; Ratcliffe and Cave 2006	Ten specimens of <i>C. abrelata</i> were collected in the flowers of an unidentified aroid or palm (Ratcliffe and Cave 2002).
Cyclocephala aequatoria Endrödi, 1963	Phytelephas aequatorialis Spruce	ECUADOR: Cānar, Cotopaxi, Esmeraldas, Manabí, Pichincha	Balslev and Henderson 1987; Ervik et al. 1999	-
Cyclocephala alazonia Ratcliffe, 2003	NO DATA	COSTA RICA: Alajuela (Reserva Biologica Monteverde, Estacion Eladios, Peñas Blancas Refuge)	Ratcliffe 2003	The two known specimens of <i>C. alazonia</i> are covered with pollen, suggesting feeding inside of a flower (Ratcliffe 2003).
	Annona muricata L.	COSTA RICA	Villalta 1988	=
	Astrocaryum alatum Loomis	PANAMA	Ratcliffe 2003	-
	Attalea butyracea (Mutis ex. L.f.) Wess. Boer	COLOMBIA	Núnez-Avellaneda and Neita 2009	=
	Bactris coloradonis L. H. Bailey	COSTA RICA: Herédia (La Selva Biological Station)	Beach 1984; Ratcliffe 2003, citing pers. comm. from J. Beach and H. Young	-
	Bactris gasipaes Kunth	COSTA RICA: Herédia (La Selva Biological Station); Limon (Guápiles, Estación Experimental de Los Diamantes)	Mora-Urpí and Solís 1980; Mora-Urpí 1982; Beach 1984; Gottsberger 1986; Rickson et al. 1990; Ratcliffe 2003, citing pers. comm. from J. Beach and H. Young	-
Cyclocephala amazona (Linnaeus, 1767)	Bactris hondurensis Standl.	COSTA RICA: Herédia (La Selva Biological Station)	Bullock 1981	-
	Cryosophila williamsii P. H. Allen	COSTA RICA: Herédia (La Selva Biological Station)	Henderson 1984; Silberbauer-Gottsberger 1990	-
	Cyclanthus bipartitus Poit. ex A. Rich.	COSTA RICA: Herédia (La Selva Biological Station)	Beach 1982	Beach (1982) reported the scarab as 6 nr. amazona. Ratcliffe (2003) recorde C. amazona from La Selva Biologica Station, thus this is probably a correct identification.
	Cymbopetalum lanugipetalum Schery	PANAMA: Colón	Murray 1993	14
	Cymbopetalum longipes Benth. ex Diels	PERU: San Martin	Murray 1993	-
	Montrichardia arborescens (L.) Schott	FRENCH GUIANA	Ponchel 2006	_
	Phytelephas seemannii O. F. Cook	COLOMBIA: Chocó	Bernal and Ervik 1996; Ervik et al. 1999	The scarab was reported as Cyclocephala amazonica (L.) (= C. amazona (L.)).
		COLOMBIA: Nariña	Pardo-Locarno et al.	

Appendix I. Continued.

	Dieffenbachia nitidipetiolata Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Young 1986; Young 1988a; Young 1988b; Young 1990; Beath	The plant was reported as D. longispatha (Croat 2004).
	Philodendron anisotomum Schott	PANAMA COSTA RICA: Herédia (La Selva Biological	1999; Ratcliffe 2003 Croat 1997, citing pers. comm. from H. Young	-
	Philodendron platypetiolatum Madison	Station) COSTA RICA: Herédia (La Selva Biological	Beath 1998	=
	Philodendron pterotum K. Koch and Augustin	Station) COSTA RICA: Herédia (La Selva Biological	Croat 1997, citing pers. comm. from H. Young	-
	Philodendron radiatum Schott	Station) COSTA RICA: Herédia (La Selva Biological	Croat 1997, citing pers.	74
	Philodendron rothschuhianum (Engl.)	Station) COSTA RICA: Herédia (La Selva Biological	Croat 1997, citing pers. comm. from H. Young	÷-
Cyclocephala amblyopsis Bates, 1888	Philodendron tripartitum (Jacq.) Schott	Station) COSTA RICA: Herédia (La Selva Biological	Croat 1997, citing pers. comm. from H. Young	-
	Syngonium sp.	Station) COSTA RICA: (Northern low lands)	Valerio 1984	=
	Xanthosoma daguense Engl.	COLOMBIA: Risaralda (Sanctuario de Fauna y Flora Otún-Quimbaya)	García-Robledo et al. 2004; García-Robledo et al. 2005	
	Xanthosoma robustum Schott	MEXICO: Chiapas (Socunusco)	Morón 1997	-
	Xanthosoma sagittifolium (L.) Schott	MEXICO: Chiapas (Socunusco) COLOMBIA: Nariña	Morón 1997 Pardo-Locarno et al.	-
	Xanthosoma sp.	(Tumaco)	2008	=
	Xanthosoma wendlandii (Schott) Standl.	COSTA RICA: San José (Granadilla de Curridabat) MEXICO: Chiapas (Cacahoatán)	Valerio 1988; Morón 1997	-
	Dieffenbachia nitidipetiolata Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Young 1990	The plant was reported as D. longispatha (Croat 2004).
Cyclocephala ampliata	Philodendron pterotum K. Koch and Augustin	COSTA RICA: Herédia (La Selva Biological Station)	Croat 1997, citing pers. comm. from H. Young	-
Bates, 1888	Philodendron radiatum Schott	COSTA RICA: Herédia (La Selva Biological Station)	Croat 1997, citing pers. comm. from H. Young; Beath 1998; Beath 1999	The scarab was reported as Cyclocephala ampliota [sic] (Beal 1999).
	Philodendron sp.	COSTA RICA	Ratcliffe 2003, citing pers. comm. from H. Young	The plant could possibly be P. pterotum or P. radiatum as reported Croat (1997).
	Cyclanthus bipartitus Poit. ex A. Rich.	COSTA RICA: Herédia (La Selva Biological Station)	Beach 1982; Ratcliffe 1992a	- Croat (1997).
	Dieffenbachia nitidipetiolata Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station) PANAMA: Colón	Young 1986; Young 1988a; Young 1990; Ratcliffe 2003	The plant was reported as D. longispatha (Croat 2004).
Cyclocephala atripes Bates, 1888	Dieffenbachia spp.	COSTA RICA: Herédia (La Selva Biological Station)	Beach 1982	Beach (1982) noted <i>C. atripes</i> on the <i>Dieffenbachia</i> spp. (possibly <i>D. nitidipetiolata</i> as described by You (1986; 1988a; 1988b)) or <i>D. tondu</i> herein.
	Dieffenbachia tonduzii Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Label data of M. Grayum	Three vouchers examined from INI
	Annona aurantiaca Barb. Rodr.	BRAZIL: Maranhão	Gottsberger 1986; Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	-
	Annona coriacea Mart.	BRAZIL: Maranhão; Minas Gerais (Indianópolis); São Paulo	Gottsberger 1986; Gottsberger and Silberbauer-Gottsberger 1988; Gottsberger 1989;Gottsberger 1999; Silberbauer-Gottsberger et al. 2003; Gottsberger and Silberbauer- Gottsberger 2006	\ \\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\

dix 1. Continued.				
	Annona cornifolia A. St Hil.	BRAZIL: Minas Gerais (Indianópolis); São Paulo (Botucatu)	Gottsberger 1986; Gottsberger 1988; Gottsberger and Silberbauer-Gottsberger 1988; Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	
	Annona crassiflora Mart.	BRAZIL: Brasília (Chapada dos Veadeiros, north of Brasilia); Goiás (Vila Propício); Minas Gerais (Indianópolis); São Paulo (Botucatu)	Gottsberger 1988; Gottsberger and Silberbauer-Gottsberger 1988; Gottsberger 1989; Gottsberger 1999; Gottsberger and Silberbauer-Gottsberger 2006; Cavalcante et al.	-
Cyclocephala atricapilla Mannerheim, 1829	Annona dioica A. St Hil.	BRAZIL: Minas Gerais (Indianópolis); São Paulo (Botucatu)	Gottsberger 1986, citing pers. obs. by Silberbauer Gottsberger; Gottsberger 1988; Gottsberger 1989; Gottsberger 1999; Gottsberger and Silberbauer-Gottsberger 2006	-
	Annona monticola Mart.	BRAZIL: Brasília; Minas Gerais (Indianópolis)	Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	-
	Annona tomentosa R. E. Fr.	BRAZIL: Brasília; Minas Gerais (Indianópolis)	Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	*
	Annona warmingiana Mello-Silva & Pirani	BRAZIL: Brasília	Gottsberger 1986; Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	-
	Caladium sp.	BRAZIL: Maranhão	Gottsberger 1986	
	Colocasia esculenta (L.) Schott	BRAZIL: São Paulo	Gottsberger 1986	The scarab was reported from cultivated C. esculenta.
	Philodendron ptarianum Steyerm. var. rugosum Bunt.	VENEZUELA: Bolívar (Canaima National Park)	Ramírez 1992	:=:
	Philodendron mello- barretoanum Burle-Marx ex G. M. Barroso	BRAZIL: Minas Gerais (Indianópolis)	Gottsberger and Silberbauer-Gottsberger 2006	-
	Xanthosoma striatipes (Kunth & C. D. Bouché) Madison	BRAZIL: São Paulo	Gottsberger 1986	=
Cyclocephala boulardi Dechambre, 1979	Bactris hirta Mart.	BRAZIL: Amazonas	Küchmeister et al. 1998	
	Dieffenbachia seguine (Jacq.) Schott	VENEZUELA: Aragua (Henri Pittier National Park)	Label data of A. Seres and N. Ramirez	A single voucher examined from USNM
	Philodendron ligulatum Schott	COSTA RICA: Herédia (La Selva Biological Station)	Label data of H. Young	A single voucher examined from INBC
Cyclocephala brevis Höhne, 1847 incertae sedis (Cyclocephala morphospecies 3 sensu Moore 2011)	Socratea sp.	VENEZUELA (Henri Pittier National Park)	Seres and Ramírez 1995	Based on other observed specimens collected by Seres and Ramirez from this locality this scarab was reported as C. sexpunctata and is Cyclocephala morphospecies 3 sensu Moore 2011
	Xanthosoma sp.	VENEZUELA (Henri Pittier National Park, Rancho Grande)	Label data of A. Seres and N. Ramirez	A single voucher examined from USNM
	Xanthosoma undipes (K. Koch & C. D. Bouché) K. Koch	VENEZUELA (Henri Pittier National Park, Rancho Grande)	Seres and Ramirez 1995; Label data of A. Seres and N. Ramirez	The scarab was identified and reported as <i>C. sexpunctata</i> (Seres and Ramirez 1995). A single voucher examined from USNM

Appendix I. Continued.

Cyclocephala brevis Höhne, 1847 incertae sedis	Cymbopetalum languipetalum Schery	PANAMA: Colón	Murray 1993	Reported as C. sexpunctata (Murra 1993).
(Cyclocephala morphospecies 4 sensu Moore 2011)	Cymbopetalum sp.	PANAMA: Colón (Btwn. Gatun and Pina)	Label data of N. A. Murray; Ratcliffe 2003	A single voucher examined from UNSM
Mode 2011)	Philodendron sp.	PANAMA: Colón (1 km E Rio Guanche Bridge)	Label data of B. Ratcliffe and M. Jameson	A single voucher examined from UNSM
	Dieffenbachia longispatha Engl. and K. Krause	PANAMA (Barro Colorado Island)	Beath 1999	The scarab was reported as C. sexpunctata which is not recorded from Barro Colorado Island (Ratclif 2003).
	Dieffenbachia nitidipetiolata Croat and Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Young 1990; Beath 1999	The scarab was reported as C. sexpunctata which is not recorded from La Selva (Ratcliffe 2003). The plant was reported as D. longispath which does not occur in La Selva (Croat 2004).
	Dieffenbachia oerstedii Schott	COSTA RICA: San José (Granadilla de Curridabat)	Valerio 1984	-
	Dieffenbachia sp.	PANAMA	Ratcliffe 2003	-
Cyclocephala brevis Höhne, 1847 incertae sedis	Philodendron fragrantissimum (Hook.) G. Don	PANAMA (Barro Colorado Island)	Beath 1998	The scarab was reported as C. sexpunctata which is not recorded Barro Colorado Island (Ratcliffe 2003).
(ambiguous records)	Philodendron platypetiolatum Madison	COSTA RICA: Herédia (La Selva Biological Station)	Beath 1998	The scarab was reported as C. sexpunctata which is not recorded Barro Colorado Island (Ratcliffe 2003).
	Philodendron pterotum K. Koch and Augustin	COSTA RICA: Herédia (La Selva Biological Station)	Croat 1997, citing pers. comm. with H. Young	The scarab was reported as C. sexpunctata which is not recorded La Selva (Ratcliffe 2003).
	Xanthosoma helleborifolium (Jacq.) Schott	PANAMA (Barro Colorado Island)	Beath 1998	The scarab was reported as C. sexpunctata which is not recorded Barro Colorado Island (Ratcliffe 2003).
	Xanthosoma mexicanum	PANAMA	Beath 1998	-
	Liebm. Xanthosoma sp.	(Barro Colorado Island) ECUADOR	Ohaus 1910	1/2
	Xanthosoma wendlandii	COSTA RICA: San José	Valerio 1988) -
	(Schott) Standl. Annona muricata L.	(Granadilla) COSTA RICA: Limón	Villalta 1988; Ratcliffe 1992a	-
Cyclocephala brittoni Endrödi, 1964	Bactris hondurensis Standl.	COSTA RICA: Herédia (La Selva Biological Station)	Bullock 1981; Ratcliffe 1992a	·-
	Rhodospatha sp.	COSTA RICA: Limón	Ratcliffe 1992a	7/2
Cyclocephala caelestis Ratcliffe and Delgado, 1990	Magnolia tamaulipana Vazquez	MEXICO: Tamaulipas (El Cielo Reserve)	Dieringer et al. 1998; Dieringer et al. 1999	-
Cyclocephala camachicola Ohaus, 1910	Xanthosoma sp.	ECUADOR (west side of Cordillera)	Ohaus 1910	-17
	Philodendron wendlandii Schott	NO DATA	Ratcliffe 2003, citing pers. comm. from H. Young	
Cyclocephala carbonaria	Dieffenbachia longispatha Engl. and K. Krause	PANAMA (Barro Colorado Island)	Beath 1999	-
Arrow, 1911	Xanthosoma helleborifolium (Jacq.) Schott	PANAMA (Barro Colorado Island)	Beath 1998	s-s
	Xanthosoma mexicanum Liebm.	PANAMA (Barro Colorado Island)	Beath 1998	- ,:
	Nymphaea glandulifera Rodschied	SURINAME	Cramer et al. 1975	-
Cyclocephala castanea (Olivier, 1789)	Nymphaea rudgeana G. Mey.	BRAZIL: Amazonas (Manaus) SURINAME	Cramer et al. 1975; Prance and Anderson 1976	- 7:
	Victoria amazonica (Poepp.) J. C. Sowerby	BRAZIL: Amazonas	von Bayern 1897; Knuth et al. 1904; Gessner 1962	-

	Caladium bicolor (Aiton)	BRAZIL: Pernambuco	Maia and Schlindwein	
	Vent.	(Goiana)	2006	-
	Gearum brasiliense N. E. Br.	BRAZIL: Tocantins (Arraias)	Gonçalves and Maia 2006	-
Cyclocephala celata	Philodendron acutatum Schott	BRAZIL: Pernambuco (Goiana, Igarassu)	Maia et al. 2010	s
Dechambre, 1980	Taccarum ulei Engl. and K. Krause	BRAZIL: Pernambuco	Maia et al. 2010, citing unpublished data of A. C. D. Maia, C. Schlindwein and M. Gibernau; Maia et al. 2012	ç <u>a</u>
Cyclocephala cearae Höhne, 1923	Taccarum ulei Engl. and K. Krause	BRAZIL: Pernambuco	Maia et al. 2012	-
	Araceae	FRENCH GUIANA	Ponchel 2006	-
	Montrichardia	FRENCH GUIANA:	Gibernau et al. 2003;	
	arborescens (L.) Schott	Kourou, Sinnamary	Ponchel 2006	
Cyclocephala colasi	Montrichardia linifera (Arruda) Schott	FRENCH GUIANA	Ponchel 2006	-
Endrödi, 1964	Philodendron melinonii Brongn. ex Regel	FRENCH GUIANA: Kourou	Gibernau et al. 2000; Ponchel 2006	120
	Philodendron	FRENCH GUIANA	Gibernau et al. 1999;	
	solimoesense A. C. Sm.	(between Kourou and Sinnamary)	Ponchel 2006; Seymour et al. 2009	-
	Cyclanthus bipartitus Poit. ex A. Rich.	COSTA RICA: Herédia (La Selva Biological Station)	Beach 1982	-
	Dieffenbachia nitidipetiolata Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Young 1988a; Young 1990	The plant was reported as D. longispatha (Croat 2004).
Cyclocephala conspicua Sharp, 1877	Dieffenbachia spp.	COSTA RICA: Herédia (La Selva Biological Station)	Beach 1982	Beach (1982) noted <i>C. conspicua</i> two <i>Dieffenbachia</i> spp. (possibly <i>nitidipetiolata</i> as described by Yo [1986; 1988a; 1988b]). The plant reported as <i>D. longispatha</i> (Cro 2004).
	Philodendron correae Croat	PANAMA: Bocas del Toro (near continental divide)	Croat 1997	=
Cyclocephala cribrata	Astrocaryum aculeatissimum (Schott) Burret	BRAZIL: São Paulo	Luederwalt 1926	17
Burmeister, 1847	Philodendron bipinnatifidum Schott ex Endl.	BRAZIL: São Paulo (Botucatu)	Gottsberger and Amaral 1984; Gottsberger 1986	v =
	Philodendron sp.	BRAZIL: São Paulo	Luederwalt 1926	
Cyclocephala discicollis Arrow, 1902	Bactris major Jacq.	COLOMBIA	Núnez-Avellaneda and Neita 2009	-
	Aphandra natalia (Balslev & A. J. Henderson) Barfod	COLOMBIA: Chocó ECUADOR: Morona- Santiago, Napo, Pastaza	Ervik et al. 1999	-
Cyclocephala discolor	Arecaceae	PERU	Ponchel 2006	-
(Herbst, 1790)	Oenocarpus bataua Mart.	COLOMBIA: Antioquia, Chocó, Meta	Nunez-Avellaneda and Rojas-Robles 2008; Núnez-Avellaneda and Neita 2009	: -
Cyclocephala distincta Burmeister, 1847	Attalea funifera Mart.	BRAZIL: Bahia	Voeks 2002	
Cyclocephala emarginata	Araceae	FRENCH GUIANA	Ponchel 2006	2
Endrödi, 1966	Philodendron solimoesense A. C. Sm.	FRENCH GUIANA	Gibernau et al. 1999	-
Cyclocephala epistomalis Bates, 1888	Nymphaea amazonum Mart. & Zucc.	BRAZIL: Mato Grosso (near Fazenda Jofre)	Prance 1980	-
	2 - 1 - 1	MEYICO	Ratcliffe and Morón	
	Asplundia sp.	MEXICO	1997	

MEXICO: Veracruz (Los

Tuxtlas)

MEXICO

MEXICO

Búrquez et al. 1987; Aguirre et al. 2011 Ratcliffe and Morón

1997

Ratcliffe and Morón

1997

The plant was reported as Astrocaryon

[sic] sp.

Cyclocephala fasciolata

Bates, 1888

Astrocaryum mexicanum

Liebm. ex Mart.

Astrocaryum sp.

Monstera sp.

		BRAZIL: Distrito	Scariot et al. 1991;	
Cyclocephala forsteri Endrödi, 1963	Acrocomia aculeata (Jacq.) Lodd. ex Mart.	Federal (Planaltina Area), Mato Grosso do Sul	Núnez-Avellaneda and Neita 2009; de Oliveira	-
		COLOMBIA	and Ávila 2011	
	Araceae	GUATEMALA: Sololá (Las Tarrales Reserve)	Label data of M. Moore	Nine vouchers deposited in WIC
	Colocasia sp.	HONDURAS: Francisco Morazán (El Zamorano)	Ratcliffe and Cave 2006	Nine vouchers deposited in WIC
	Dieffenbachia longispatha Engl. and K. Krause	PANAMA (Barro Colorado Island)	Beath 1999	
	Dieffenbachia nitidipetiolata Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station) PANAMA: Colón	Young 1986; Young 1988a; Young 1988b; Young 1990; Beath 1999; Ratcliffe 2003	The plant was reported as D. longispatha (Croat 2004).
Cyclocephala gravis Bates, 1888	Montrichardia arborescens (L.) Schott	VENEZUELA: Guárico State (near Calabozo)	Ramirez and Brito 1992	
Dates, 1000	Philodendron grandipes K. Krause	COSTA RICA: Herédia (La Selva Biological Station)	Young 1986; Croat 1997; Croat 1997, citing pers. comm. with H.	= =
	11.11.000	PANAMA: San Blas (Nusagandi)	Young	
	Xanthosoma helleborifolium (Jacq.) Schott	PANAMA (Barro Colorado Island)	Beath 1998	-
	Xanthosoma mexicanum Liebm.	PANAMA (Barro Colorado Island)	Beath 1998	-
Cyclocephala gregaria	Xanthosoma daguense	COLOMBIA: Risaralda	García-Robledo et al.	
Heyne and Taschenberg, 1907	Engl.	(Sanctuario de Fauna y Flora Otún-Quimbaya)	2004; García-Robledo et al. 2005	#
Cyclocephala guianae Endrödi, 1969	Oenocarpus bacaba Mart.	BRAZIL: Amazonas	Küchmeister et al. 1998	
SERVICE BOOK OF VENO	NA - 1 NO - 1	BRAZIL: Amazonas	Endrödi 1975; Prance	
Cyclocephala hardyi Endrödi, 1975	Victoria amazonica (Poepp.) J. C. Sowerby	GUAYANA: Upper Takutu-Upper Essequibo (Karanambu Ranch)	and Arias 1975; Seymour and Matthews 2006	- :
Cyclocephala iani Ratcliffe, 1992b	Annona nitida Mart.	BRAZIL: Amazonas	Ratcliffe 1992b	
Cyclocephala inca Endrödi, 1966	Attalea insignis (Mart.) Drude	COLOMBIA	Núnez-Avellaneda and Neita 2009	227
Cyclocephala jalapensis Casey, 1915	Magnolia schiedeana Schltl.	MEXICO: Veracruz (Xalapa area)	Dieringer and Delgado 1994; Dieringer and Espinosa 1994	21
	Dieffenbachia nitidipetiolata Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Young 1986; Young 1988a; Young 1990	The plant was reported as <i>D. longispatha</i> (Croat 2004).
	Philodendron radiatum Schott	NO DATA	Croat 1997	8
Cyclocephala kaszabi Endrödi, 1964	Philodendron rothschuhianum (Engl.) Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Young 1987	÷
	Philodendron tripartitum (Jacq.) Schott	COSTA RICA: Herédia (La Selva Biological Station)	Croat 1997, citing pers. comm. from H. Young	=
	Xanthosoma daguense Engl.	COLOMBIA: Risaralda (Sanctuario de Fauna y Flora Otún-Quimbaya)	García-Robledo et al. 2004; García-Robledo et al. 2005	⊕ :
Cyclocephala laminata Burmeister, 1847	Cereus pernambucensis Lem.	BRAZIL: Rio de Janeiro	Rosa et al. 1995; Rosa et al. 1999; Lachance et al. 2001	-
Cyclocephala	Annona crassilflora Mart.	BRAZIL: Goiás (Vila Propicio)	Cavalcante et al. 2009	a i
latericia Höhne, 1923	Araceae	BRAZIL: Pará	Martínez 1968	The scarab was reported as

	Dieffenbachia nitidipetiolata Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Young 1986; Young 1988a; Young 1990	The plant was reported as D. longispatha (Croat 2004).
	Philodendron cretosum Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Ratcliffe 2003	=
Cyclocephala ligyrina Bates, 1888	Philodendron jodavisianum G. S. Bunting	PANAMA: Panamá	Croat 1997	8
	Philodendron pterotum K. Koch and Augustin	PANAMA (Former Canal Zone)	Croat 1997	=
	Philodendron radiatum Schott	NO DATA	Croat 1997	<u> </u>
	Philodendron rothschuhianum (Engl.) Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Ratcliffe 2003	_
Cyclocephala literata Burmeister, 1847	Annona crassilflora Mart.	BRAZIL: São Paulo	Gottsberger 1986; Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	.π.·
	Magnolia ovata (A. St Hil.) Spreng.	BRAZIL: São Paulo	Gottsberger 1986; Gottsberger 1989; Gottsberger et al. 2012	≥;
	Acacia pennata (L.) Willd.	NO DATA	Ratcliffe and Morón 1997	=:
	Ficus sp.	NO DATA	Morón 1997 Ratcliffe and Morón	
Cyclocephala lunulata	Hibiscus rosa-sinensis L.	NO DATA	1997	.
Burmeister, 1847	Psidium sp. Pithecellobium dulce	NO DATA	Morón 1997 Ratcliffe and Morón	The plant was asserted as
	(Roxb.) Benth.	NO DATA	1997	The plant was reported as Pitecellobium [sic] dulce.
	Pithecellobium sp.	COLOMBIA: Valle del Cauca	Stechauner-Rohringer and Pardo-Locarno 2010	<->>
Cyclocephala lutea Endrödi, 1966	Cactaceae	BRAZIL: Pará	Martínez 1968	-
	Araceae	GUATEMALA: Solóla (Las Tarrales Reserve)	Label data of M. Moore	Four vouchers deposited in WIC.
	Malmea depressa (Baill.) R. E. Fr.	MEXICO: Michoacán	Murray 1993	1=)
	Philodendron jodavisianum G. S. Bunting	PANAMA: Panamá	Croat 1997	-
Cyclocephala mafaffa Burmeister, 1847	Philodendron giganteum Schott	Guadeloupe archipelago	Ponchel 2006	-
Bullioset, 1047	Xanthosoma robustum Schott	MEXICO: Chiapas (Cacahoatán and Chiapa de Corzco)	Morón 1997; Morón 1997, citing pers. comm. from Beutelspacher); Ratcliffe and Morón 1997	
	Xanthosoma wendlandii (Schott) Standl.	COSTA RICA: Guanacaste (Nicoya)	Valerio 1988	-
Cyclocephala marginalis Kirsch, 1870 [1871]	Attalea butyracea (Mutis ex. L.f.) Wess. Boer	COLOMBIA	Núnez-Avellaneda and Neita 2009	11-0
2113011, 1070 [1071]	Attalea microcarpa Mart. Acrocomia aculeata	BRAZIL: Amazonas	Küchmeister et al. 1998	= (c
Cyclocephala	(Jacq.) Lodd. ex Mart.	BRAZIL: Distrito Federal (Planaltina Area)	Scariot et al. 1991	=
mecynotarsis Höhne, 1923	Attalea geraensis Barb. Rodr.	BRAZIL	Gottsberger and Silberbauer-Gottsberger 2006	-
Cyclocephala melanae	Philodendron schottianum	COSTA RICA: Cartago	Croat 1997	

	Annua andana Mast	BRAZIL: São Paulo	Gottshaman 1096	
	Annona coriacea Mart.	BRAZIL: Sao Paulo	Gottsberger 1986	-
	Brugmansia arborea (L.) Steud. or Brugmansia x candida Pers. or Brugmansia suaveolens (Humb, & Bonpl, ex Willd.) Bercht, & J. Presl	BRAZIL: São Paulo ECUADOR	Ohaus 1910; Gottsberger 1986	The plant was reported as Datura arborea without assigning authorship. The name D. arborea was used by three authors and is a synonym of the species listed to the left. The identity of the association with Brugmansia sis ambiguous.
Cyclocephala melanocephala (Fabricius,	Brugmansia insignis (Barb. Rodr.) Lockwood ex R. E. Schult.	COLOMBIA	Hay et al. 2012	:-
1775)	Cactaceae	FRENCH GUIANA	Ponchel 2006	: -
	Datura innoxia Mill.	USA: New Mexico	Cockerell 1897	
	Datura sp.	USA: Arizona,	Moore 1937; Saylor	
		California, New Mexico	1945; Linsley 1960	-
	Datura wrightii Regel	USA: Arizona	Raguso et al. 2003	(-
	Kielmeyera variabilis Mart. & Zucc.	BRAZIL: São Paulo	Gottsberger 1986	-
	Magnolia ovata (A. St Hil.) Spreng.	BRAZL: São Paulo	Gottsberger 1986	-
	Mandevilla longiflora (Desf.) Pichon	BRAZIL: São Paulo	Gottsberger 1986	-
	Porcelia magnifructa (Schery) R.E. Fr.	PANAMA: Veraguas	Murray 1993	:=
Cyclocephala metrica Steinheil, 1874	Verbesina encelioides (Cav.) Benth. & Hook.f. ex A. Gray	ARGENTINA: Salta	Hayward 1946	Reported to feed on the seeds of V. encelioides.
Cyclocephala munda Kirsch, 1870 [1871]	Xanthosoma poeppigii Schott	PERU: Loreto (Estación Biológica Madre Selva)	García-Robledo et al. 2005	:=
	Monstera adansonii Schott var. adansonii	COSTA RICA: Puntarenas (Monteverde)	Ratcliffe 2003, citing pers. comm. from A. Smith	-
	Philodendron brenesii Standl.	COSTA RICA: San José (vicinity of Vara Blanca)	Croat 1997	=
	Philodendron sp.	NO DATA	Valerio 1984	-
Cyclocephala nigerrima Bates, 1888	Philodendron tysonii Croat	PANAMA: Chiriquí (near continental divide)	Croat 1997	=
	Xanthosoma undipes (K. Koch & C. D. Bouché) K. Koch	COSTA RICA: Guanacaste (Peñas Blancas), Puntarenas (Monteverde)	Goldwasser 1987; Goldwasser 2000; García-Robledo et al. 2005, citing pers. comm. with T. Croat	The plant was reported as Xanthoson robustum Schott (García-Robledo e al. 2005, citing pers. comm. with T. Croat).
Cyclocephala ohausiana Höhne, 1923	Annona coriacea Mart.	BRAZIL: Minas Gerais, São Paulo	Gottsberger 1986; Gottsberger 1988; Gottsberger and Silberbauer-Gottsberger 1988; Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	\(\frac{1}{2}\)
	Xanthosoma striatipes (Kunth & C. D. Bouché) Madison	BRAZIL: São Paulo	Gottsberger 1986; Gottsberger 1989	-
Cyclocephala octopunctata Burmeister, 1847	Annona crassilflora Mart.	BRAZIL: Goiás (Goiána and Vila Propício)	Cavalcante et al. 2009	75
Durmeister, 1847	Annona dioica A. St Hil.	BOLIVIA: Santa Cruz	Label data of uncredited collector	Single voucher examined from UNSI
Cuala canhala annihum	Helianthus sp. (girsasol)	ARGENTINA	Hayward 1946	=
Cyclocephala ovulum Bates, 1888	Inga sp.	ECUADOR: Napo (Yasuni Research Station)	Label data of Mary Liz Jameson	Plant voucher examined from WICI
Cyclocephala	Annona coriacea Mart.	BRAZIL: São Paulo	Gottsberger 1989	-
paraguayensis Arrow,	Kielmeyera variabilis		PARTITION OF THE PARTIT	
1903	Mart. & Zucc.	BRAZIL: São Paulo	Gottsberger 1986	÷

	Annona montana Macfad.	BRAZIL: Amazonas (Manaus)	Webber 1981	The scarab was reported from cultivated A. montana.
Cyclocephala picipes (Olivier, 1789)	Annona muricata L.	BRAZIL: Amazonas (Manaus)	Webber 1981	The scarab was reported from cultivated A. muricata.
	Annona nitida Mart.	BRAZIL: Amazonas (Manaus)	Webber 1981	7-1
Cyclocephala picta Burmeister, 1847	Xanthosoma robustum Schott	MEXICO: Veracruz	Morón 1977	K— I
Cyclocephala prolongata Arrow, 1902	Attalea amygdalina Kunth	COLOMBIA	Núnez-Avellaneda and Neita 2009	<u>,−</u>
Cyclocephala nr. putrida Burmeister, 1847	Nymphaea lasiophylla Mart. & Zucc.	BRAZIL (northeastern)	Wiersema 1987	84
Cyclocephala	Aphandra natalia (Balslev & A. J. Henderson) Barfod	COLOMBIA: Chocó ECUADOR: Morona- Santiago, Napo, Pustaza	Ervik et al. 1999	9 <u>4</u> (
quadripunctata Höhne, 1923	Attalea insignis (Mart.) Drude	COLOMBIA	Núnez-Avellaneda and Neita 2009	n= 1
	Phytelephas macrocarpa Ruiz & Pav.	COLOMBIA: Chocó ECUADOR: Napo	Ervik et al. 1999	-
	Annona aurantiaca Barb. Rodr.	BRAZIL: Mato Grosso	Silberbauer-Gottsberger et al. 1997	Anecdotal, citing Gottsberger (198 and Gottsberger and Silberbauer- Gottsberger (1988). This association was not verifiable in cited literature.
	Annona coriacea Mart.	BRAZIL: Mato Grosso, Minas Gerais, São Paulo	Gottsberger 1986; Gottsberger 1989; Silberbauer-Gottsberger et al. 1997; Gottsberger and Silberbauer- Gottsberger 2006	The scarab was reported as C. inpunctata (Gottsberger 1986)
	Annona cornifolia A. St Hil.	BRAZIL: Minas Gerais (Indianópolis); São Paulo (Botucatu)	Gottsberger 1986; Gottsberger 1988; Gottsberger and Silberbauer-Gottsberger 1988; Gottsberger 1989; Gottsberger 1999; Gottsberger and Silberbauer-Gottsberger 2006	The scarab was reported as C. inpunctata (Gottsberger 1986; Gottsberger 1988)
Cyclocephala quatuordecimpunctata	Annona crassiflora Mart.	BRAZIL: Brasília (Chapada dos Veadeiros, north of Brasilia); Goiás; Minas Gerais (Indianópolis); São Paulo (Botucatu)	Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	9 4
Mannerheim, 1829	Annona dioica A. St Hil.	BRAZIL: Mato Grosso; Minas Gerais (Indianópolis); São Paulo (Botucatu)	Gottsberger 1986, citing pers. obs. by Silberbauer- Gottsberger; Gottsberger 1988; Gottsberger 1989; Silberbauer-Gottsberger et al. 1997; Gottsberger and Silberbauer- Gottsberger 2006	The scarab was reported as C. inpunctata (Gottsberger 1986)
	Annona hybrid forms 1 & 3	BRAZIL: Mato Grosso	Silberbauer-Gottsberger et al. 1997	-
	Annona malmeana R. E. Fr. x Annona coriacea Mart.	BRAZIL: Mato Grosso	Gottsberger and Silberbauer-Gottsberger 2006	- 2
	Annona monticola Mart.	BRAZIL: Minas Gerais	Gottsberger and Silberbauer-Gottsberger 2006	-
	Annona tomentosa R. E. Fr.	BRAZIL: Brasília; Minas Gerais (Indianópolis)	Gottsberger 1989; Gottsberger 1999; Gottsberger and Silberbauer-Gottsberger 2006	<u> -</u> %
	NO DATA	BRAZIL	Mannerheim 1829	些)
122 2 020020 B	Montrichardia	FRENCH GUIANA	Ponchel 2006	= 3
Cyclocephala quercina Burmeister, 1847	arborescens (L.) Schott Nymphaeaceae	FRENCH GUIANA	Ponchel 2006	

Appendix I. Continued.

Cyclocephala rubescens Bates, 1891	Philodendron grayumii Croat	PANAMA: Coclé (near El Copé)	Croat 1997	C. rubescens is not recorded in Panama (Ratcliffe 2003).
Cyclocephala rufovaria Апоw, 1911	Araceae	FRENCH GUIANA	Ponchel 2006	***
	Araceae	BRAZIL: Manaus (Reserva Ducke) FRENCH GUIANA	Label data of I. Gottsberger; Ponchel 2006	A single voucher examined from UNSM
	Arecaceae	BRAZIL: Manaus (Reserva Ducke)	Label data of S. Vidal	Two vouchers examined from deposited UNSM
Cyclocephala rustica (Olivier, 1789)	Caladium bicolor (Aiton) Vent.	SURINAME FRENCH GUIANA: Karou	Pellmyr 1985; Label data of M. Gibernau	Two vouchers examined from i
	Dieffenbachia seguine (Jacq.) Schott	FRENCH GUIANA (Nouragues)	Label data of M. Gibernau	Five voucher specimens examine from UNSM
	Philodendron callosum K. Krause	NO DATA	Croat 1997	_
	Philodendron ptarianum Steyerm.	NO DATA	Croat 1997	The plant voucher is listed as Ram 1163 by Croat (1997). In the Trop database Ramirez 1163 is a specir of <i>Philodendron callosum</i> K. Kra
Cyclocephala santaritae	Attalea insignis (Mart.) Drude	COLOMBIA	Núnez-Avellaneda and Neita 2009	
Ratcliffe, 1992a	Oenocarpus sp.	ECUADOR: Napo	Label data of H. Balslev and A. Henderson	Three voucher specimens exami from UNSM
Cyclocephala sarpedon Ratcliffe, 1992b	Oenocarpus bacaba Mart.	BRAZIL: Amazonas	Küchmeister et al. 1998	#-S
Cyclocephala sexpunctata	Araceae	GUATEMALA: Sololá (Las Tarrales Reserve); Huehuetenago (Zapote) MEXICO: Veracruz (Catemaco, Pipipan, Parque de la Flora y Fauna Silvestre Tropical)	Label data of M. Moore; Label data of F. Capistran; Bates 1888	Two specimens deposited in WICI single voucher examined from UV (Capistran).
Laporte, 1840 incertae sedis (Cyclocephala morphospecies 1 sensu Moore 2011)	Xanthosoma robustum Schott	MEXICO: Chiapas (Cacahoatán); Guerrero (Mochitlán, Achauizolta)	Morón 1997; Label data of L. Delgado	A single voucher examined from UVGC. Morón (1997) reported to beetle as C. sexpunctata.
	Xanthosoma sagittifolium (L.) Schott	MEXICO: Chiapas (Cacahoatán)	Morón 1997	-
	Xanthosoma sp.	GUATEMALA: Quetzaltenango (El Palmar near Finca El Faro)	Label data of E. Cano	A single voucher examined from UVGC.
	Xanthosoma wendlandii (Schott) Standl.	MEXICO: Chiapas (Cacahoatán)	Morón 1997	-
Cyclocephala sexpunctata Laporte, 1840 incertae sedis (Cyclocephala	Alocasia macrorrhizos (L.) G. Don	COSTA RICA: San José (Parque del Este)	Label data of uncredited collector; Valerio 1984	Eight voucher specimens examir from UNSM
	Araceae	PANAMA: Chiriquí (La Fortune, Quebrada Al Trail)	Label data of J. Ashe & A. Brooks	A single voucher examined from KSEM
morphospecies 2 sensu Moore 2011)	Philodendron tripartitum (Jacq.) Schott	COSTA RICA: San José (Parque del Este)	Label data of uncredited collector	Two vouchers examined from UN
1110010 2011)	Xanthosoma sp.	(San Ramon, Rio S. Lorencito)	Label data of A. Solís	A single voucher examined from INBC

	Philodendron grandipes K. Krause	NO DATA	Croat 1997	-
	Philodendron grayumii Croat	PANAMA: Coclé (near El Copé)	Croat 1997	**
	Philodendron sagittifolium Liebm.	PANAMA: Panamá	Croat 1997	-
Cyclocephala sexpunctata	Philodendron solimoesense A. C. Sm.	FRENCH GUIANA	Gibernau et al. 1999	-
Laporte, 1840 incertae sedis (ambiguous records)	Xanthosoma poeppigii Schott	PERU: Loreto (Estación Biológica Madre Selva)	García-Robledo et al. 2005	-
	Xanthosoma undipes (K. Koch & C. D. Bouché) K. Koch	COSTA RICA: Cartago (San Ramón de la Unión), Guanacaste (Peñas Blancas), Puntarenas (Monteverde)	Goldwasser 1987; Seres and Ramírez 1995; Goldwasser 2000; García-Robledo <i>et al.</i> 2005	Goldwasser (1987; 2000) reported the plant as <i>Xanthosoma robustum</i> Schot (García-Robledo <i>et al.</i> 2005, citing pers. comm. with T. Croat).
	Xanthosoma wendlandii (Schott) Standl.	COSTA RICA: Herédia (Santo Domingo); Alajuela (Alajuela)	Valerio 1988	=
Cyclocephala simulatrix	Philodendron solimoesense A. C. Sm.	FRENCH GUIANA	Ponchel 2006	=
Höhne, 1923	Philodendron squamiferum Poepp.	FRENCH GUIANA: Kourou	Gibernau and Barabé 2002	(=
	Annona purpurea Moç & Sessé ex Dunal	MEXICO: Michoacán	Murray 1993	
	Cymbopetalum baillonii R. E. Fr.	MEXICO: Veracruz	Murray 1993	=
	Cymbopetalum costaricense (Donn. Sm.) R. E. Fr.	COSTA RICA: Herédia (La Selva Biological Station)	Schatz 1985	u=
Cyclocephala sparsa	Cymbopetalum gracile R. E. Fr.	MEXICO: Guerrero	Murray 1993	10
Arrow, 1902	Cymbopetalum hintonii Lundell	MEXICO: Jalisco	Murray 1993	#E
	Cymbopetalum torulosum G. E. Schatz	COSTA RICA: Herédia (La Selva Biological Station)	Bawa et al. 1985a; Bawa et al. 1985b; Schatz 1985; Kress and Beach 1994	*
	Malmea aff. depressa (Baill.) R. E. Fr.	MEXICO: Veracruz (Estacion Biológica Los Tuxtlas)	Schatz 1987)

Α	p	рe	n	di	X	ı.	Со	ntir	nued.
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Cyclocephala spp.

Annona montana Macfad.	BRAZIL: Amazonas (Amazonia)	Webber 1981	The scarab was reported from cultivated A. montana.
Annona muricata L.	BRAZIL: Amazonas (Manaus)	Webber 1981	The scarab was reported from cultivated A. muricata.
Annona sp. ex aff. Annona paludosa Aubl.	BRAZIL (Amazonia, near Paricatuba)	Gottsberger 1989	—»
Annona Section Pilannona	NO DATA	Schatz 1987	-
Aphandra natalia (Balslev & A. J. Henderson) Barfod	ECUADOR: Morona- Santiago (20 km south of Sucua)	Ervik 1993	-
Attalea spectabilis Mart.	BRAZIL: Amazonas (Ducke Forest Reserve)	Küchmeister et al. 1993	-
Bactris gasipaes Kunth	PERU: Huánaco (Pachitea)	Listabarth 1992	1 =8
Bactris hirta var. pectinata (Mart.) Govaerts	BRAZIL: Manaus (Reserve 1501 of Biological Dynamics of Forest Fragments Project)	Henderson et al. 2000	-
Bactris sp.	PERU: Huanaco (Pachitea)	Listabarth 1992	
Carludovica drudei Mast.	COSTA RICA: Puntarenas	Anderson and Gómez-P.	-
Carludovica palmata Ruiz & Pav.	COSTA RICA: Puntarenas	Anderson and Gómez-P. 1997	-
Cymbopetalum stenophyllum Donn. Sm.	MEXICO: Chiapas	Murray 1993	7-8
Dieffenbachia pittieri Engl. & K. Krause	NO DATA	Pellmeyr 1985, citing pers. comm. from J. Beach	The plant was reported as D . piltie [sic].
Duguetia spixiana Mart.	PERU: Madre de Dios (Tambopata)	Maas et al. 2003	1-1
Echinopsis ancistrophora Speg. subsp. ancistrophora	ARGENTINA	Slumpberger et al. 2009	
Elaeis oleifera (Kunth) Cortés	NO DATA	Hardon 1969, citing unpublished data of J. J. Hardon	
Hancornia speciosa Gomes	BRAZIL: Minas Gerais	Gottsberger 1986	1=0
Magnolia ovata (A. St Hil.) Spreng.	BRAZL: São Paulo	Gottsberger 1986	(-)
Oenocarpus bacaba Mart.	BRAZIL: Amazonas	Küchmeister et al. 1998	n - >
Opuntia monacantha Haw.	BRAZIL: Santa Catarina (Florianópolis)	Lenzi and Inácio Orth 2011	ren
Philodendron aurantiifolium subsp. aurantiifolium Schott	COSTA RICA: Herédia (La Selva Biological Station)	Grayum 1996	1=0
Philodendron ptarianum Steyerm. var. rugosum Bunt.	VENEZUELA: Bolívar (Canaima National Park)	Ramírez 1989	Two unidentified Cyclocephala species came to P. ptarianum. On scarab species was indentified as a tricopilla [sic] (= C. atricapilla) Ramírez 1992.
Porcelia spp.	NO DATA	Schatz 1987, citing pers. comm. from P. J. M. Maas	-
Pouteria sp.	BRAZIL: Minas Gerais	Gottsberger 1986	
Syagrus sancona (Kunth) H. Karst.	COLOMBIA	Núnez-Avellaneda and Neita 2009	->
Syngonium triphyllum Birdsey ex Croat	COSTA RICA	Croat 1981, citing pers. comm. from T. Ray	-
Tabernaemontana sp.	BRAZIL: Minas Gerais	Gottsberger 1986	
Wettinia quinaria (O. F. Cook & Doyle) Burret	COLOMBIA: Chocó (El Amargal Biological Station)	Núñez et al. 2005	
Xanthosoma undipes (K. Koch and C. D. Bouché) K. Koch	VENEZUELA (Henri Pittier National Park)	Seres and Ramírez 1995	
Xanthosoma wendlandii (Schott) Standl.	COSTA RICA: Guanacaste (Carmona de	Valerio 1988	-

Appendix I. Continued.

	Astrocaryum alatum Loomis	COSTA RICA: Herédia (La Selva Biological Station)	Bullock 1981	-
	Annona muricata L.	COSTA RICA	Villalta 1988; Ratcliffe 2003	-
	Bactris coloradonis L. H.	COSTA RICA	Ratcliffe 2003	=
Cyclocephala stictica Burmeister, 1847	Bailey Bactris hondurensis Standl.	COSTA RICA: Herédia (La Selva Biological Station)	Bullock 1981	-
	Oenocarpus bataua Mart.	COLOMBIA: Antioquia, Chocó, Meta	Nunez-Avellaneda and Rojas-Robles 2008	=
	Xanthosoma sagittifolium (L.) Schott	MEXICO: Chiapas (Cacahoatán)	Morón 1997	-
	Xanthosoma wendlandii (Schott) Standl.	MEXICO: Chiapas (Cacahoatán)	Morón 1997	i e
	Cyclanthus bipartitus Poit. ex A. Rich.	VENEZUELA (Henri Pittier National Park)	Seres and Ramírez 1995	8
	Dieffenbachia nitidipetiolata Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Young 1986; Young 1988a; Young 1990	C. tutilina is not recorded in Costa Rica (Ratcliffe 2003). The plant wa reported as D. longispatha (Croat 2004).
Cyclocephala tutilina	Dieffenbachia seguine (Jacq.) Schott	VENEZUELA: Aragua (Henri Pittier National Park)	Ratcliffe and Cave 2006; Label data of A. Seres and N. Ramirez	The plant was reported as <i>D. seguin</i> [sic] (Ratlcliffe and Cave 2006). A single voucher was examined from USNM
Burmeister, 1847	Dieffenbachia sp.	VENEZUELA (Henri Pittier National Park)	Seres and Ramírez 1995	9
	Philodendron macroglossum Schott	VENEZUELA (Henri Pittier National Park)	Seres and Ramírez 1995	-
	Xanthosoma sp.	ECUADOR VENEZUELA (Henri Pittier National Park)	Ohaus 1910; Label data of A. Seres and N. Ramirez	A single voucher examined from USNM
	Xanthosoma undipes (K. Koch and C. D. Bouché) K. Koch	VENEZUELA (Henri Pittier National Park)	Seres and Ramírez 1995	-
Cyclocephala tylifera Höhne, 1923	Philodendron squamiferum Poepp.	FRENCH GUIANA: Kourou	Gibernau and Barabé 2002; Ponchel 2006	=
11011100, 1720	Annona foetida Mart.	BRAZIL: Amazonas (Manaus)	Gottsberger 1999, citing unpublished data of A. C. Weber and G. Gottsberger	70
	Annona montana Macfad.	NO DATA	Gottsberger et al. 1998	2
	Bactris hirta Mart.	BRAZIL: Amazonas	Küchmeister et al. 1998	-
Cuala combala condata	Cymbopetalum euneurum N. A. Murray	BRAZIL: Amazonas (Ducke Forest Reserve)	Webber and Gottsberger 1993	-
(Olivier, 1789)	Duguetia asterotricha (Diels) R. E. Fr.	BRAZIL: Manaus	Label data of G. Gottsberger	A single voucher examined from UNSM
	Duguetia riparia Huber	BRAZIL: Amazonas	Küchmeister et al. 1998	-
	Duguetia ulei (Diels) R. E. Fr.	BRAZIL: Amazonas	Küchmeister et al. 1998	=
	Malmea manausensis Maas & Miralha	NO DATA	Gottsberger et al. 1998	-
	Montrichardia arborescens (L.) Schott	FRENCH GUIANA	Ponchel 2006	5
Cyclocephala variabilis Burmeister, 1847	Attalea geraensis Barb. Rodr.	BRAZIL: São Paulo	Gottsberger 1986	
Cyclocephala varians	Montrichardia arborescens (L.) Schott	FRENCH GUIANA: Kourou, Sinnamary	Gibernau et al. 2003; Ponchel 2006	=
Burmeister, 1847	Montrichardia linifera (Arruda) Schott	FRENCH GUIANA	Ponchel 2006	
	Nymphaeaceae	FRENCH GUIANA	Ponchel 2006	
Cyclocephala variolosa	Philodendron bipinnatifidum Schott ex Endl.	BRAZIL: São Paulo (Botucatu)	Gottsberger and Amaral 1984; Gottsberger 1986	-
Burmeister, 1847	Philodendron sp.	BRAZIL: São Paulo (Botucatu)	Gottsberger and Amaral 1984	8
Cyclocephala vestita Höhne, 1923	Annona muricata L.	BRAZIL (northeastern)	Cavalcante 2000; Maia et al. 2010, citing unpublished data of Maia, Schlindwein and Gibernau	=
	Montrichardia	FRENCH GUIANA:	Gibernau et al. 2003;	

	Corythophora rimosa W. A. Rodrigue	BRAZIL: Amazonas (Manaus)	Prance 1976	=
	Eschweilera decolorans Sandwith	BRAZIL: Amazonas (Manaus)	Prance 1976) =
	Eschweilera sp.	BRAZIL: Amazonas (Manaus)	Prance 1976	#E
	Lecythis lurida (Miers) S. A. Mori	BRAZIL: Amazonas (Manaus)	Prance 1976	=
Cyclocephala verticalis Burmeister, 1847	Nymphaea amazonum Mart. & Zucc.	SURINAME	Cramer et al. 1975	=
Daimeister, 1017	Nymphaea conardii Wiersema	VENEZUELA: Barinas (Sosa)	Wiersema 1987	-
	Nymphaea rudgeana G. Mey.	BRAZIL: Pará (Belém) SURINAME	Cramer et al. 1975; Prance and Anderson 1976	-
	Victoria amazonica (Poepp.) J. C. Sowerby	BRAZIL: Amazonas GUYANA: Upper Takutu- Upper Essequibo (Karanambu Ranch)	Prance and Arias 1975; Seymour and Matthews 2006	-
Cyclocephala williami Ratcliffe, 1992a	Psidium sp.	COSTA RICA	Ratcliffe 1992a; Ratcliffe 2003	-
Dyscinetus nr. plicatus (Burmeister, 1847)	Annona sp. ex aff. Annona densicoma Mart.	BRAZIL (lower Rio Purús)	Gottsberger 1989	The scarab was attracted to floral odors but was not collected in inflorescences (Gottsberger 1989)
	Dieffenbachia nitidipetiolata Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station) PANAMA	Young 1986; Young 1988a; Young 1988b; Young 1990; Beath 1999; Ratcliffe 2003	The plant was reported as D. longispatha (Croat 2004).
	Dieffenbachia sp.	COSTA RICA: Herédia (La Selva Biological Station)	Label data of M. Grayum	A single voucher examined from INBC
	Philodendron anisotomum Schott	COSTA RICA: Herédia (La Selva Biological Station)	Croat 1997, citing pers. comm. from H. Young	-
	Philodendron aurantiifolium Schott	COSTA RICA: Herédia (La Selva Biological Station)	Label data of M. Grayum; Grayum 1996	A single voucher examined from INBC. Grayum (1996) reported th beetle as <i>E. proba</i> Sharp, which do not occur in Costa Rica (Rateliffe 2003)
	Philodendron brevispathum Schott	COSTA RICA: Herédia (La Selva Biological Station)	Grayum 1996; Croat 1997	Beetle was reported as <i>E. proba</i> Sha (Grayum 1996; Croat 1997), whice does not occur in Costa Rica (Ratcli 2003)
Erioscelis columbica Endrödi, 1966	Philodendron grandipes K. Krause	COSTA RICA: Limón	Croat 1997	=
	Philodendron guttiferum Kunth	COSTA RICA: Herédia (La Selva Biological Station)	Morón 1997, citing pers. comm. from A. Solís	-
	Philodendron jodavisianum G. S. Bunting	COSTA RICA: Herédia (La Selva Biological Station)	Croat 1997, citing pers. comm. from H. Young	_
	Philodendron radiatum Schott	COSTA RICA: Herédia (La Selva Biological Station)	Croat 1997, citing pers. comm. from H. Young	-
	Philodendron rothschuhianum (Engl.) Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Croat 1997, citing pers. comm. from H. Young	7
	Philodendron tripartitum (Jacq.) Schott	COSTA RICA: Herédia (La Selva Biological Station)	Croat 1997, citing pers. comm. from H. Young	4 4
	Syngonium schottianum Wendl. ex Schott	COSTA RICA: Herédia (La Selva Biological Station)	Morón 1997, citing pers. comm. from A. Solís; Beath 1998; Label data of M. Grayum	Three vouchers examined from INI

	Araceae	BRAZIL: Pará	Martinez 1968	-
	NO DATA	BRAZIL	Mannerheim 1829	-
Erioscelis emarginata (Mannerheim, 1829)	Philodendron bipinnatifidum Schott ex Endl.	BRAZIL: São Paulo (around Botucatu) PARAGUAY (Villa Encarnacion)	Schrottky 1910; Gottsberger 1986; Gottsberger and Amaral 1984; Gottsberger and Silberbauer-Gottsberger 1991	-
	Xanthosoma striatipes (Kunth & C. D. Bouché) Madison	PARAGUAY (Villa Encarnacion)	Schrottky 1908; Schrottky 1910	This association was questioned by Gottsberger and Amaral (1984).
P. J. J. Gl.	Dieffenbachia seguine (Jacq.) Schott	FRENCH GUIANA (Nouragues Field Station)	Label data of M. Gibernau	28 vouchers examined from UNSM
Erioscelis proba Sharp, 1877	Montrichardia arborescens (L.) Schott	FRENCH GUIANA: Kourou, Sinnamary	Gibernau et al. 2003	-
	Philodendron squamiferum Poepp.	FRENCH GUIANA	Ponchel 2006	-
	Astrocaryum alatum Loomis	COSTA RICA: Herédia (La Selva Biological Station)	Bullock 1981	-
Mimeoma acuta (Arrow,	Bactris coloradonis L. H. Bailey	COSTA RICA: Herédia (La Selva Biological Station)	Beach 1984; Ratcliffe 2003, citing pers. comm. with J. Beach and H. Young	-
1902)	Bactris hondurensis Standl.	COSTA RICA: Herédia (La Selva Biological Station)	Bullock 1981; Ratcliffe 2003, citing pers. comm. with J. Beach and H. Young	-
	Bactris longiseta H. Wendl. ex Burret	COSTA RICA: Herédia (La Selva Biological Station)	Bullock 1981	-
Mimeoma englemani Ratcliffe, 1977	Bactris spp.	PANAMA	Ratcliffe 2003	Ratcliffe (2003) did not state these associations occur in Panama, although M. englemani is currently known only from Panama.
Mimeoma maculata (Burmeister, 1847)	Astrocaryum paramaca Mart.	FRENCH GUIANA	Ponchel 2006; Ponchel 2010	The plant was reported as Astrocarya paramaka [sic].
Mimeoma signatoides (Höhne, 1923)	Socratea sp.	VENEZUELA (Henri Pittier National Park)	Label data of A. Serez and N. Ramirez	A single voucher examined from USNM
Peltonotus malayensis Arrow, 1910	Epipremnum falcifolium Engl.	BRUNEI	Jameson and Wada 2004	-
Peltonotus nasutus Arrow, 1910	Amorphophallus paeoniifolius (Dennst.) Nicolson	THAILAND: Changwat (Thung Yai Wildlife Sanctuary)	Grimm 2009	-
Ruteloryctes morio (Fabricius, 1798)	Nymphaea lotus L.	BENIN CÔTE d'IVOIRE: Zanzan (Comoé National Park) SENEGAL: Kaolack, Tambacounda	Ervik and Knudsen 2003; Hirthe and Porembski 2003; Krell et al. 2003	-
	Nymphaea sp.	West Indies (erroneous label data)	Fabricius 1798	Time:
Cyclocephalini	Echinopsis ancistrophora Speg. subsp. ancistrophora	ARGENTINA	Schlumpberger and Raguso 2008	Reported as a destructive, nocturns scarab. Based on photographs, the ti beetles are probably cyclocephaline (in litt. with B. Schlumpberger, Apr. 2011).
	Rhodospatha sp.	COSTA RICA: Herédia (La Selva Biological Station)	Schatz 1990	-

	Bactris gasipaes Kunth	PERU: Huánuco	Listabarth 1996	-
	Bactris maraja Mart.	PERU: Huánuco	Listabarth 1996	This scarab was reported as a most rare visitor (Listabarth 1996).
	Bactris bifida Mart.	PERU: Huánuco	Listabarth 1996	This scarab was reported as a most rare visitor (Listabarth 1996).
_	Bognera recondita (Madison) Mayo & Nicolson	BRAZIL: Amazonas (Lago Cauxi near Atalaia)	Gonçalves and Maia 2006; Bogner 2008, citing upublished data of E. G. Gonçalves	The authors did not explicity state the locality of the association data, although extensive observations of B recondita were made only in Amazonas, Brazil
Dynastinae	Homalomena sp.	MALAYA	Grayum 1990, citing pers. comm. From G. E. Schatz	This is likely a misidentification. Peltonotus was not in the Cyclocephalini prior to 2006 (Smith 2006). These beetles could be Parastasia spp. (Scarabaeidae: Rutelinae), species of which are known visitors of Homalomena spp. on Borneo (Malaysia) (Momose et al. 1998; Chen et al. 2011).
	Monstera oreophila Madison	PANAMA: Chiriquí	Grayum 1990	-
	Ammandra decasperma O. F. Cook	COLOMBIA: Valle del Cauca (Buenaventura)	Cook 1927	-
	Annona montana Macfad.	COSTA RICA: Herédia (La Selva Biological Station)	Bawa et al. 1985b	=
	Asimina sp.	NO DATA	Gottsberger 1988	-
	Attalea speciosa Mart.	BRAZIL: Maranhão (Lago Verde); Pará (Serra Norte, Canoal)	Anderson et al. 1988	-
	Chlorospatha spp.	NO DATA	Madison 1981	-
	Evodianthus funifer (Poit.) Lindm. subsp. funifer	PERU (Lower Río Llullapichus, Panguana Field Station)	Gottsberger 1991	-
	Homalomena hammelii Croat and Grayum	NO DATA	Grayum 1984	***
	Philodendron bipinnatifidum Schott ex Endl.	BRAZIL: Minas Gerais (Lagoa Santa)	Warming 1883	-
Scarabaeidae	Philodendron davidsonii Croat	NO DATA	Grayum 1984	-
	Philodendron grandipes K. Krause	NO DATA	Grayum 1984	-
	Philodendron ligulatum Schott	NO DATA	Grayum 1984	-
	Philodendron venosum (Willd. Ex Schult. & Schult.f.) Croat	NO DATA	Grayum 1984	-
	Philodendron radiatum Schott	NO DATA	Grayum 1984	12
	Philodendron rothschuhianum (Engl.) Croat & Grayum	NO DATA	Grayum 1984	-
	Porcelia sp.	NO DATA	Gottsberger 1988	<u> </u>
	Syngonium schottianum H. Wendl. ex Schott	NO DATA	Grayum 1984	-
	Xanthosoma robustum Schott	NO DATA	Grayum 1984	

	Philodendron acuminatissimum Engl.	NO DATA	Madison 1979	-
Coleoptera	Philodendron cruentospathum Madison	NO DATA	Madison 1979, citing pers. comm. from C. H. Dodson	Inflorenscences of this plant species rotate to capture water after anthesis which is a strategy to drive beetles ou of the spathe (Madison 1979).
	Philodendron senatocarpium Madison	NO DATA	Madison 1979	Inflorescences of this plant species are often filled with water which is a strategy to drive beetles out the spathe (Madison 1979).
	Philodendron venosum (Willd. ex Schult. & Schult.f.) Croat	NO DATA	Madison 1979	Inflorescences of this plant species are often filled with water which is a strategy to drive beetles out the spathe Scarabs have been reported from <i>P. venosum</i> (Grayum1984).
	Rhodospatha forgetii N. E. Br.	NO DATA	Grayum 1986, citing pers. comm. from G. Schatz	The beetles could be cyclocephalines based on the observations of Schatz (1990).
	Xanthosoma sagittifolium (L.) Schott	NO DATA	Madison 1979	The plant species displays a "drowning" strategy similar to Philodendron (Madison 1979).
Evidence of beetle feeding	Nymphaea oxypetala Planch.	VENEZUELA	Wiersema 1987	=

Appendix 2. Cyclocephaline synonyms reported in the floral association literature.					
Synonym (Reported Name)	Reference				
Cyclocephala signata (Fabricius, 1781)	Mora-Urpí and Solís 1980; Mora-Urpí 1982; Gottsberger 1986				
Cyclocephala pubescens Burmeister, 1847	Valerio 1984; Valerio 1988				
Cyclocephala mollis Endrödi, 1963	Prance 1980				
Cyclocephala maffafa [sic] grandis Burmeister, 1847	Ponchel 2006				
	Cockerell 1897; Moore 1937; Saylor 1945; Linsley 1960				
Dichromia dimidiata (Burmeister, 1847)	Cocketell 1897, Woole 1937, Saylor 1943, Ellistey 1900				
	Synonym (Reported Name) Cyclocephala signata (Fabricius, 1781) Cyclocephala pubescens Burmeister, 1847 Cyclocephala mollis Endrödi, 1963				

Appendix 3. Plant synonyms reported in floral association literature and on voucher specimen label data.

Valid Name	Synonym (Reported Name)	Reference
Annona warmingiana Mello-Silva & Pirani	Annona pygmaea (Warm.) Warm.	Gottsberger 1986; Gottsberger 1989
Astrocaryum aculeatissimum (Schott) Burret	Astrocaryum aryi Mart.	Luederwalt 1926
Attalea speciosa Mart.	Orbignya phalerata Mart.	Anderson et al. 1988
Attalea spectabilis Mart.	Orbignya spectabilis (Mart.) Burret	Küchmeister et al. 1993
Bactris coloradonis L. H. Bailey	Bactris porschiana Burret	Beach 1984; Ratcliffe 2003
Bactris hirta var. pectinata (Mart.) Govaerts	Bactris hirta var. spruceana (Trail) A.J.Hend.	Henderson et al. 2000
Bactris hondurensis Standl.	Bactris wendlandiana Burret	Bullock 1981; Ratcliffe 1992a
Bactris maraja Mart.	Bactris monticola Barb. Rodr.	Listabarth 1996
Brugmansia sp.	Datura arborea (no author)	Ohaus 1910; Gottsberger 1986
Cryosophila williamsii P. H. Allen	Cryosophila albida Bartlett	Henderson 1984; Silberbauer-Gottsberger 1990
Datura innoxia Mill.	Datura meteloides DC. ex Dunal	Cockerell 1897
Lecythis lurida (Miers) S. A. Mori	Holopyxidium jaranum Huber ex Ducke	Prance 1976
Mandevilla longiflora (Desf.) Pichon	Macrosiphonia longiflora (Desf.) Mül. Arg.	Gottsberger 1986
Magnolia ovata (A. StHil.) Spreng.	Talauma ovata A. StHil, 1824	Gibbs et al. 1977; Gottsberger 1986; Gottsberger 1989
Oenocarpus sp.	Jessenia sp.	Label data of Balslev and Henderson. Three specimens deposited in UNSM
Nymphaea glandulifera Rodschied	Nymphaea blanda var. fenzliana (Lehm.) Casp.	Cramer et al. 1975
Philodendron bipinnatifidum Schott ex Endl.	Philodendron selloum C. Koch	Gottsberger 1986; Gottsberger and Amaral 1984; Gottsberger and Silberbauer-Gottsberger 1991
Philodendron venosum (Willd. ex Schult. & Schult.f.) Croat	Philodendron karstenianum Schott	Grayum 1984
Phytelephas aequatorialis Spruce	Palandra aequatorialis (Spruce) O. F. Cook	Balslev and Henderson 1987
Tabernaemontana sp.	Peschiera sp.	Gottsberger 1986
Victoria amazonica (Poepp.) J. C. Sowerby	Victoria regia Lindl.	von Bayern 1897; Knuth et al. 1904; Gessner 1962; Martínez 1968
Xanthosoma mexicanum Liebm.	Xanthosoma pilosum K. Koch & Augustin	Beath 1998
Xanthosoma sagittifolium (L.) Schott	Xanthosoma violaceum Schott	Morón 1997
Xanthosoma striatipes (Kunth & C. D. Bouché) Madison	Caladium striatipes (Kunth & C. D. Bouché) Schott	Schrottky 1910; Gottsberger 1986; Gottsberger 1989
Xanthosoma wendlandii (Schott) Standl.	Xanthosoma hoffmanni [sic] (Schott) Schott	Morón 1997

Appendix 4. Unavailable and unresolved plant names from the floral association literature and voucher specimen label data.

Valid Name	Reported Name	Reference or Label Data
Alocasia macrorrhizos (L.) G. Don (pers. comm. with T. B. Croat, May 2011)	Xanthosoma macrorrhizas	Valerio 1984; Label data of unaccredited collector
Dieffenbachia tonduzii Croat & Grayum (pers. comm.	Dieffenbachia longivaginata	Label data of M. Grayum. Beetle
with T. B. Croat and M. Grayum, May 2011)	Croat & Grayum ined.*	voucher specimens deposited at INBC
Philodendron ligulatum Schott (pers. comm. with T. B. Croat and M. Grayum, May 2011)	Philodendron atlanticum Croat & Grayum	Grayum 1984; Label data of H. Young
Philodendron ptarianum Stey. or Philodendron rugosum Bogner & G.S.Bunting	Philodendron ptarianum Stey. var. rugosum Bunt.	Ramírez 1989; Ramirez 1992
Unresolved	Cereus pernambucensis Lem.	Rosa et al. 1995; Rosa et al. 1999; Lechance et al. 2001
Unresolved	Kielmeyera variabilis Mart. & Zucc.	Gottsberger 1986
Unresolved	Malmea manausensis Maas & Miralha	Gottsberger et al. 1998

^{*}ined: a name only that appears in an unpublished manuscript and is thus invalid.