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## 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to promote research by updating nomenclature, identifying inconsistencies in the data, and reporting previously unpublished data.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 vicariance hypotheses, host plant shifts, and mutualisms with angiosperms.

**Keywords:** Cantharophily, Scarabaeidae, Dynastinae, Araceae, Arecaceae, Annonaceae, Nymphaeaceae

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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 pan-tropical 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). Cy-

clocephaline visitation of dicot flowers is poorly known and little studied.

Cyclocephaline floral associations have been reported in journals, books, and monographs since the late 18<sup>th</sup> 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](http://www.bioone.org)), BIOSIS Previews® (<http://apps.webofknowledge.com/>), JSTOR ([www.jstor.org](http://www.jstor.org)), and Biodiversity Heritage Library ([www.biodiversitylibrary.org](http://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](http://www.tropicos.org)) and The Plant List ([www.plantlist.org](http://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 species-level identifications that were reported by several authors. Particularly, this included specimens 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 floral 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 Nebraska State Museum (authoritatively 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 non-specific 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-

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 Previously unpublished cyclocephaline beetle floral association data.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

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 dubious record, see Appendix 1].

Plant Taxa	Scarab Genera
NYMPHAELES	
Nymphaeaceae	
Nymphaea	Cyclocephala Dejean Ruteloryctes Arrow
Victoria	Arriguttia Martínez Chalepides Casey Cyclocephala
MAGNOLIALES	
Annonaceae	
Annona	Cyclocephala Dyscinetus Harold (?)
Cymbopetalum	Cyclocephala
Duguetia	Cyclocephala
Malmea	Cyclocephala
Porcelia	Cyclocephala
Magnoliaceae	
Magnolia	Augoderia Burmeister (?) Cyclocephala
ALISMATALES	
Araceae	
Alocasia	Cyclocephala
Amorphophallus	Peltonotus Burmeister
Caladium	Cyclocephala
Colocasia	Cyclocephala
Dieffenbachia	Cyclocephala Erioscelis Burmeister
Epipremnum	Peltonotus
Gearum	Cyclocephala
Monstera	Cyclocephala
Montrichardia	Aspidolea Bates Cyclocephala Erioscelis
Philodendron	Cyclocephala Erioscelis
Rhodospatha	Cyclocephala
Syngonium	Cyclocephala Erioscelis
Taccarum	Cyclocephala
Xanthosoma	Cyclocephala Erioscelis
Araceae undetermined	Arriguttia Martínez
PANDANALES	
Cyclanthaceae	
Asplundia	Cyclocephala
Carludovica	Cyclocephala
Cyclanthus	Cyclocephala
ARECALES	
Arecaceae	
Acrocomia	Cyclocephala
Aphandra	Cyclocephala
Astrocaryum	Cyclocephala Mimeoma Casey
Attalea	Cyclocephala
Bactris	Cyclocephala Mimeoma
Cryosophila	Cyclocephala
Elaeis	Cyclocephala



**Table 2.** Continued.

<i>Oenocarpus</i>	<i>Aspidolea</i>
	<i>Cyclocephala</i>
<i>Phytelphas</i>	<i>Cyclocephala</i>
<i>Socratea</i>	<i>Cyclocephala</i>
	<i>Mimeoma</i>
<i>Syagrus</i>	<i>Cyclocephala</i>
<i>Wettinia</i>	<i>Cyclocephala</i>
<b>FABALES</b>	
<b>Fabaceae</b>	
<i>Acacia</i>	<i>Cyclocephala</i>
<i>Pithecellobium</i>	<i>Cyclocephala</i>
<i>Inga</i>	<i>Cyclocephala</i>
<b>ROSALES</b>	
<b>Moraceae</b>	
<i>Ficus</i>	<i>Cyclocephala</i>
<b>MALPIGHIALES</b>	
<b>Calophyllaceae</b>	
<i>Kielmeyera</i>	<i>Cyclocephala</i>
<b>MYRTALES</b>	
<b>Myrtaceae</b>	
<i>Psidium</i>	<i>Cyclocephala</i>
<b>MALVALES</b>	
<b>Malvaceae</b>	
<i>Hibiscus</i>	<i>Cyclocephala</i>
<b>CARYOPHYLLALES</b>	
<b>Cactaceae</b>	
<i>Cereus</i>	<i>Cyclocephala</i>
<i>Echinopsis</i>	<i>Cyclocephala</i>
<i>Opuntia</i>	<i>Cyclocephala</i>
<b>ERICALES</b>	
<b>Lecythidaceae</b>	
<i>Corythophora</i>	<i>Cyclocephala</i>
<i>Eschweilera</i>	<i>Cyclocephala</i>
<i>Lecythis</i>	<i>Cyclocephala</i>
<b>Sapotaceae</b>	
<i>Pouteria</i>	<i>Cyclocephala</i>
<b>ASTERALES</b>	
<b>Asteraceae</b>	
<i>Helianthus</i>	<i>Cyclocephala</i>
<i>Verbesina</i>	<i>Cyclocephala</i>
<b>SOLANALES</b>	
<b>Solanaceae</b>	
<i>Brugmansia</i>	<i>Cyclocephala</i>
<i>Datura</i>	<i>Cyclocephala</i>
<b>GENTIANALES</b>	
<b>Apocynaceae</b>	
<i>Hancornia</i>	<i>Cyclocephala</i>
<i>Mandevilla</i>	<i>Cyclocephala</i>
<i>Tabernaemontana</i>	<i>Cyclocephala</i>

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 macrorrhizas* (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, Araceae, 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 with cyclocephaline beetles (large pollen grains with sticky exudates, sturdy and funnel-shaped 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 cyclocephalines 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 systems arose in 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, differs 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 monacantha* 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*, and *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 congeners. A single inflorescence may host large crowds of beetles, often more than 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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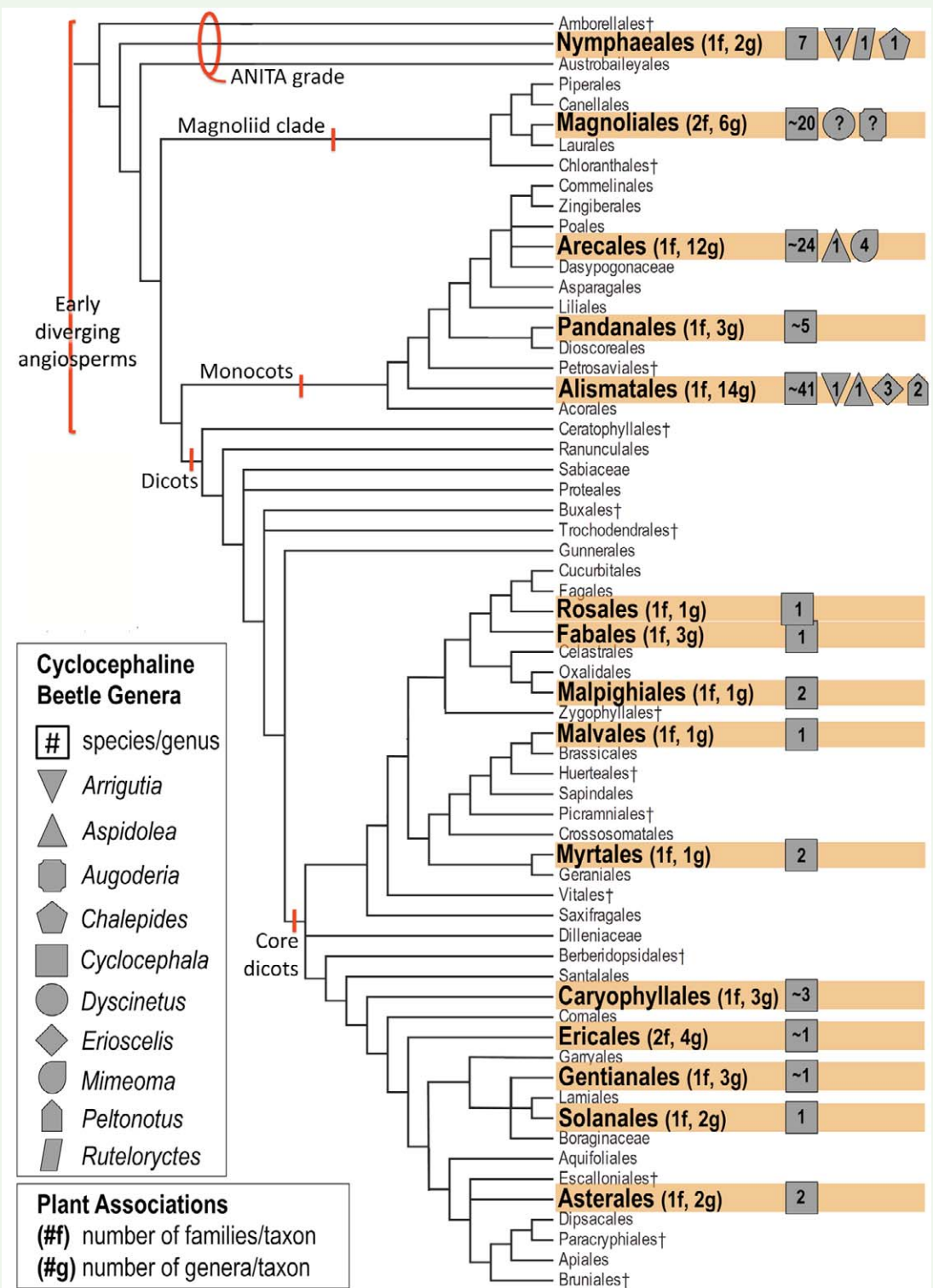
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**Figure 1.** Cyclocephaline beetle genera and their associations with angiosperm plant lineages (plant phylogeny from APGIII 2009). Icons denote beetle genera that are associated with angiosperm plant lineages. Numbers in the icons indicate the number of species for each beetle genus. If the number of beetle species is unresolved due to conflict in the literature, this is indicated with ~ symbol (the number may be X ± 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 I for data. High quality figures are available online.

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

Beetle Taxon	Plant Taxon	Geographic Locality	References	Remarks
<i>Arriguttia brevissima</i> (Arrow, 1911)	Araceae	FRENCH GUIANA	Ponchel 2006	–
	<i>Victoria amazonica</i> (Poepp.) J. C. Sowerby	BRAZIL: Pará	Martínez 1968	–
<i>Aspidolea fuliginea</i> Burmeister, 1847	<i>Oenocarpus bataua</i> Mart.	COLOMBIA: Antioquia, Chocó, Meta	Núñez-Avellaneda and Rojas-Robles 2008	–
<i>Aspidolea quadrata</i> Endrödi, 1980	<i>Montrichardia arborescens</i> (L.) Schott	FRENCH GUIANA: Kourou, Sinnamary	Gibernau <i>et al.</i> 2003; Ponchel 2006	–
<i>Augoderia nitidula</i> Burmeister, 1847 or <i>Cyclocephala</i> nr. <i>emarginata</i> Endrödi, 1966 or <i>Cyclocephala literata</i> Burmeister, 1847	<i>Magnolia ovata</i> (A. St.-Hil.) Spreng.	BRAZIL: Minas Gerais, São Paulo	Gibbs <i>et al.</i> 1977	Gibbs <i>et al.</i> (1977) stated that the scarab was <i>A. nitidula</i> , but the figure legend reported the scarab species as <i>Cyclocephala</i> nr. <i>emarginata</i> Endrödi, 1966. Gottsberger (1986) reported the scarab species as <i>C. literata</i> .
<i>Chalepides dilatatus</i> (Mannerheim, 1829)	NO DATA	BRAZIL	Mannerheim 1829	–
<i>Chalepides</i> sp.	<i>Victoria cruziana</i> A. D. Orb.	ARGENTINA: Corrientes	Valla and Cirino 1972	–
<i>Cyclocephala abrelata</i> 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).
<i>Cyclocephala aequatoria</i> Endrödi, 1963	<i>Phytelephas aequatorialis</i> Spruce	ECUADOR: Cñar, Cotopaxi, Esmeraldas, Manabí, Pichincha	Balslev and Henderson 1987; Ervik <i>et al.</i> 1999	–
<i>Cyclocephala alazonia</i> Ratcliffe, 2003	NO DATA	COSTA RICA: Alajuela (Reserva Biológica Monteverde, Estación 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).
<i>Cyclocephala amazona</i> (Linnaeus, 1767)	<i>Annona muricata</i> L.	COSTA RICA	Villalta 1988	–
	<i>Astrocaryum alatum</i> Loomis	PANAMA	Ratcliffe 2003	–
	<i>Attalea butyracea</i> (Mutis ex L.f.) Wess. Boer	COLOMBIA	Núñez-Avellaneda and Neita 2009	–
	<i>Bactris coloradonis</i> L. H. Bailey	COSTA RICA: Heredia (La Selva Biological Station)	Beach 1984; Ratcliffe 2003, citing pers. comm. from J. Beach and H. Young	–
	<i>Bactris gasipaes</i> Kunth	COSTA RICA: Heredia (La Selva Biological Station); Limón (Guápiles, Estación Experimental de Los Diamantes)	Mora-Urpí and Solís 1980; Mora-Urpí 1982; Beach 1984; Gottsberger 1986; Rickson <i>et al.</i> 1990; Ratcliffe 2003, citing pers. comm. from J. Beach and H. Young	–
	<i>Bactris hondurensis</i> Standl.	COSTA RICA: Heredia (La Selva Biological Station)	Bullock 1981	–
	<i>Cryosophila williamsii</i> P. H. Allen	COSTA RICA: Heredia (La Selva Biological Station)	Henderson 1984; Silberbauer-Gottsberger 1990	–
	<i>Cyclanthus bipartitus</i> Poit. ex A. Rich.	COSTA RICA: Heredia (La Selva Biological Station)	Beach 1982	Beach (1982) reported the scarab as <i>C. nr. amazona</i> . Ratcliffe (2003) recorded <i>C. amazona</i> from La Selva Biological Station, thus this is probably a correct identification.
	<i>Cymbopetalum lanugipetalum</i> Schery	PANAMA: Colón	Murray 1993	–
	<i>Cymbopetalum longipes</i> Benth. ex Diels	PERU: San Martín	Murray 1993	–
	<i>Montrichardia arborescens</i> (L.) Schott	FRENCH GUIANA	Ponchel 2006	–
	<i>Phytelephas seemannii</i> O. F. Cook	COLOMBIA: Chocó	Bernal and Ervik 1996; Ervik <i>et al.</i> 1999	The scarab was reported as <i>Cyclocephala amazonica</i> (L.) (= <i>C. amazona</i> (L.)).
	<i>Phytelephas</i> sp.	COLOMBIA: Nariña (Tumaco)	Pardo-Locarno <i>et al.</i> 2008	–



## Appendix I. Continued.

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

## Appendix I. Continued.

<i>Cyclocephala atricapilla</i> Mannerheim, 1829	<i>Annona cornifolia</i> 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	—
	<i>Annona crassiflora</i> Mart.	BRAZIL: Brasília (Chapada dos Veadeiros, north of Brasília); 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 <i>et al.</i> 2009	—
	<i>Annona dioica</i> 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	—
	<i>Annona monticola</i> Mart.	BRAZIL: Brasília; Minas Gerais (Indianópolis)	Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	—
	<i>Annona tomentosa</i> R. E. Fr.	BRAZIL: Brasília; Minas Gerais (Indianópolis)	Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	—
	<i>Annona warmingiana</i> Mello-Silva & Pirani	BRAZIL: Brasília	Gottsberger 1986; Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	—
	<i>Caladium</i> sp.	BRAZIL: Maranhão	Gottsberger 1986	—
	<i>Colocasia esculenta</i> (L.) Schott	BRAZIL: São Paulo	Gottsberger 1986	The scarab was reported from cultivated <i>C. esculenta</i> .
	<i>Philodendron ptarianum</i> Steyerm. var. <i>rugosum</i> Bunt.	VENEZUELA: Bolívar (Canaima National Park)	Ramírez 1992	—
	<i>Philodendron mello-barretoanum</i> Burle-Marx ex G. M. Barroso	BRAZIL: Minas Gerais (Indianópolis)	Gottsberger and Silberbauer-Gottsberger 2006	—
	<i>Xanthosoma striatipes</i> (Kunth & C. D. Bouché) Madison	BRAZIL: São Paulo	Gottsberger 1986	—
<i>Cyclocephala boulardi</i> Dechambre, 1979	<i>Bactris hirta</i> Mart.	BRAZIL: Amazonas	Küchmeister <i>et al.</i> 1998	—
<i>Cyclocephala brevis</i> Höhne, 1847 <i>incertae sedis</i> ( <i>Cyclocephala</i> morphospecies 3 <i>sensu</i> Moore 2011)	<i>Dieffenbachia seguine</i> (Jacq.) Schott	VENEZUELA: Aragua (Henri Pittier National Park)	Label data of A. Seres and N. Ramirez	A single voucher examined from USNM
	<i>Philodendron ligulatum</i> Schott	COSTA RICA: Herédia (La Selva Biological Station)	Label data of H. Young	A single voucher examined from INBC
	<i>Socratea</i> sp.	VENEZUELA (Henri Pittier National Park)	Seres and Ramirez 1995	Based on other observed specimens collected by Seres and Ramirez from this locality this scarab was reported as <i>C. sexpunctata</i> and is <i>Cyclocephala</i> morphospecies 3 <i>sensu</i> Moore 2011
	<i>Xanthosoma</i> sp.	VENEZUELA (Henri Pittier National Park, Rancho Grande)	Label data of A. Seres and N. Ramirez	A single voucher examined from USNM
	<i>Xanthosoma undipes</i> (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.

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

## Appendix I. Continued.

<i>Cyclocephala celata</i> Dechambre, 1980	<i>Caladium bicolor</i> (Aiton) Vent.	BRAZIL: Pernambuco (Goiana)	Maia and Schlindwein 2006	–
	<i>Gearum brasiliense</i> N. E. Br.	BRAZIL: Tocantins (Arraias)	Gonçalves and Maia 2006	–
	<i>Philodendron acutatum</i> Schott	BRAZIL: Pernambuco (Goiana, Igarassu)	Maia <i>et al.</i> 2010	–
	<i>Taccarum ulei</i> Engl. and K. Krause	BRAZIL: Pernambuco	Maia <i>et al.</i> 2010, citing unpublished data of A. C. D. Maia, C. Schlindwein and M. Gibernau; Maia <i>et al.</i> 2012	–
<i>Cyclocephala cearae</i> Höhne, 1923	<i>Taccarum ulei</i> Engl. and K. Krause	BRAZIL: Pernambuco	Maia <i>et al.</i> 2012	–
<i>Cyclocephala colasi</i> Endrödi, 1964	Araceae	FRENCH GUIANA	Ponchel 2006	–
	<i>Montrichardia</i> <i>arborescens</i> (L.) Schott	FRENCH GUIANA: Kourou, Sinnamary	Gibernau <i>et al.</i> 2003; Ponchel 2006	–
	<i>Montrichardia linifera</i> (Arruda) Schott	FRENCH GUIANA	Ponchel 2006	–
	<i>Philodendron melinonii</i> Brongn. ex Regel	FRENCH GUIANA: Kourou	Gibernau <i>et al.</i> 2000; Ponchel 2006	–
	<i>Philodendron</i> <i>solimoesense</i> A. C. Sm.	FRENCH GUIANA (between Kourou and Sinnamary)	Gibernau <i>et al.</i> 1999; Ponchel 2006; Seymour <i>et al.</i> 2009	–
<i>Cyclocephala conspicua</i> Sharp, 1877	<i>Cyclanthus bipartitus</i> Poit. ex A. Rich.	COSTA RICA: Herédia (La Selva Biological Station)	Beach 1982	–
	<i>Dieffenbachia</i> <i>nitidipetiolata</i> Croat & Grayum	COSTA RICA: Herédia (La Selva Biological Station)	Young 1988a; Young 1990	The plant was reported as <i>D.</i> <i>longispatha</i> (Croat 2004).
	<i>Dieffenbachia</i> spp.	COSTA RICA: Herédia (La Selva Biological Station)	Beach 1982	Beach (1982) noted <i>C. conspicua</i> on two <i>Dieffenbachia</i> spp. (possibly <i>D.</i> <i>nitidipetiolata</i> as described by Young [1986; 1988a; 1988b]). The plant was reported as <i>D. longispatha</i> (Croat 2004).
	<i>Philodendron correae</i> Croat	PANAMA: Bocas del Toro (near continental divide)	Croat 1997	–
<i>Cyclocephala cribrata</i> Burmeister, 1847	<i>Astrocaryum</i> <i>aculeatissimum</i> (Schott) Burret	BRAZIL: São Paulo	Luederwalt 1926	–
	<i>Philodendron</i> <i>bipinnatifidum</i> Schott ex Endl.	BRAZIL: São Paulo (Botucatu)	Gottsberger and Amaral 1984; Gottsberger 1986	–
	<i>Philodendron</i> sp.	BRAZIL: São Paulo	Luederwalt 1926	–
<i>Cyclocephala discicollis</i> Arrow, 1902	<i>Bactris major</i> Jacq.	COLOMBIA	Núñez-Avellaneda and Neita 2009	–
<i>Cyclocephala discolor</i> (Herbst, 1790)	<i>Aphandra natalia</i> (Balslev & A. J. Henderson) Barfod	COLOMBIA: Chocó ECUADOR: Morona- Santiago, Napo, Pastaza	Ervik <i>et al.</i> 1999	–
	Areaceae	PERU	Ponchel 2006	–
	<i>Oenocarpus bataua</i> Mart.	COLOMBIA: Antioquia, Chocó, Meta	Núñez-Avellaneda and Rojas-Robles 2008; Núñez-Avellaneda and Neita 2009	–
<i>Cyclocephala distincta</i> Burmeister, 1847	<i>Attalea funifera</i> Mart.	BRAZIL: Bahia	Voeks 2002	–
<i>Cyclocephala emarginata</i> Endrödi, 1966	Araceae	FRENCH GUIANA	Ponchel 2006	–
	<i>Philodendron</i> <i>solimoesense</i> A. C. Sm.	FRENCH GUIANA	Gibernau <i>et al.</i> 1999	–
<i>Cyclocephala epistomalis</i> Bates, 1888	<i>Nymphaea amazonum</i> Mart. & Zucc.	BRAZIL: Mato Grosso (near Fazenda Jofre)	Prance 1980	–
<i>Cyclocephala fasciolata</i> Bates, 1888	<i>Asplundia</i> sp.	MEXICO	Ratcliffe and Morón 1997	–
	<i>Astrocaryum mexicanum</i> Liebm. ex Mart.	MEXICO: Veracruz (Los Tuxtlas)	Búrquez <i>et al.</i> 1987; Aguirre <i>et al.</i> 2011	–
	<i>Astrocaryum</i> sp.	MEXICO	Ratcliffe and Morón 1997	The plant was reported as <i>Astrocaryon</i> [sic] sp.
	<i>Monstera</i> sp.	MEXICO	Ratcliffe and Morón 1997	–



## Appendix 1. Continued.

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

## Appendix I. Continued.

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



## Appendix I. Continued.

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

## Appendix I. Continued.

<i>Cyclocephala picipes</i> (Olivier, 1789)	<i>Annona montana</i> Macfad.	BRAZIL: Amazonas (Manaus)	Webber 1981	The scarab was reported from cultivated <i>A. montana</i> .
	<i>Annona muricata</i> L.	BRAZIL: Amazonas (Manaus)	Webber 1981	The scarab was reported from cultivated <i>A. muricata</i> .
	<i>Annona nitida</i> Mart.	BRAZIL: Amazonas (Manaus)	Webber 1981	—
<i>Cyclocephala picta</i> Burmeister, 1847	<i>Xanthosoma robustum</i> Schott	MEXICO: Veracruz	Morón 1977	—
<i>Cyclocephala prolongata</i> Arrow, 1902	<i>Attalea amygdalina</i> Kunth	COLOMBIA	Núñez-Avellaneda and Neita 2009	—
<i>Cyclocephala</i> nr. <i>putrida</i> Burmeister, 1847	<i>Nymphaea lasiophylla</i> Mart. & Zucc.	BRAZIL (northeastern)	Wiersema 1987	—
<i>Cyclocephala quadripunctata</i> Höhne, 1923	<i>Aphandra natalia</i> (Balslev & A. J. Henderson) Barfod	COLOMBIA: Chocó ECUADOR: Morona-Santiago, Napo, Pustaza	Ervik <i>et al.</i> 1999	—
	<i>Attalea insignis</i> (Mart.) Drude	COLOMBIA	Núñez-Avellaneda and Neita 2009	—
	<i>Phytelephas macrocarpa</i> Ruiz & Pav.	COLOMBIA: Chocó ECUADOR: Napo	Ervik <i>et al.</i> 1999	—
<i>Cyclocephala quatuordecimpunctata</i> Mannerheim, 1829	<i>Annona aurantiaca</i> Barb. Rodr.	BRAZIL: Mato Grosso	Silberbauer-Gottsberger <i>et al.</i> 1997	Anecdotal, citing Gottsberger (1989) and Gottsberger and Silberbauer-Gottsberger (1988). This association was not verifiable in cited literature.
	<i>Annona coriacea</i> Mart.	BRAZIL: Mato Grosso, Minas Gerais, São Paulo	Gottsberger 1986; Gottsberger 1989; Silberbauer-Gottsberger <i>et al.</i> 1997; Gottsberger and Silberbauer-Gottsberger 2006	The scarab was reported as <i>C. inpunctata</i> (Gottsberger 1986)
	<i>Annona cornifolia</i> 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 <i>C. inpunctata</i> (Gottsberger 1986; Gottsberger 1988)
	<i>Annona crassiflora</i> Mart.	BRAZIL: Brasília (Chapada dos Veadeiros, north of Brasília); Goiás; Minas Gerais (Indianópolis); São Paulo (Botucatu)	Gottsberger 1989; Gottsberger and Silberbauer-Gottsberger 2006	—
	<i>Annona dioica</i> 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 <i>et al.</i> 1997; Gottsberger and Silberbauer-Gottsberger 2006	The scarab was reported as <i>C. inpunctata</i> (Gottsberger 1986)
	<i>Annona</i> hybrid forms 1 & 3	BRAZIL: Mato Grosso	Silberbauer-Gottsberger <i>et al.</i> 1997	—
	<i>Annona malmeana</i> R. E. Fr. x <i>Annona coriacea</i> Mart.	BRAZIL: Mato Grosso	Gottsberger and Silberbauer-Gottsberger 2006	—
	<i>Annona monticola</i> Mart.	BRAZIL: Minas Gerais	Gottsberger and Silberbauer-Gottsberger 2006	—
	<i>Annona tomentosa</i> R. E. Fr.	BRAZIL: Brasília; Minas Gerais (Indianópolis)	Gottsberger 1989; Gottsberger 1999; Gottsberger and Silberbauer-Gottsberger 2006	—
	NO DATA	BRAZIL	Mannerheim 1829	—
<i>Cyclocephala quercina</i> Burmeister, 1847	<i>Montrichardia arborescens</i> (L.) Schott	FRENCH GUIANA	Ponchel 2006	—
	Nymphaeaceae	FRENCH GUIANA	Ponchel 2006	—
<i>Cyclocephala rondoniana</i> Ratcliffe, 1992b	<i>Attalea attaleoides</i> (Barb. Rodr.) Wess. Boer	BRAZIL: Amazonas	Küchmeister <i>et al.</i> 1998	—



**Appendix 1.** Continued.

<i>Cyclocephala rubescens</i> Bates, 1891	<i>Philodendron grayumii</i> Croat	PANAMA: Coclé (near El Copé)	Croat 1997	<i>C. rubescens</i> is not recorded in Panama (Ratcliffe 2003).
<i>Cyclocephala rufovaria</i> Arrow, 1911	Araceae	FRENCH GUIANA	Ponchel 2006	–
<i>Cyclocephala rustica</i> (Olivier, 1789)	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) SURINAME	Label data of S. Vidal	Two vouchers examined from deposited UNSM
	<i>Caladium bicolor</i> (Aiton) Vent.	FRENCH GUIANA: Karou	Pellmyr 1985; Label data of M. Gibernau	Two vouchers examined from in UNSM
	<i>Dieffenbachia seguine</i> (Jacq.) Schott	FRENCH GUIANA (Nouragues)	Label data of M. Gibernau	Five voucher specimens examined from UNSM
	<i>Philodendron callosum</i> K. Krause	NO DATA	Croat 1997	–
	<i>Philodendron ptarianum</i> Steyerm.	NO DATA	Croat 1997	The plant voucher is listed as Ramirez 1163 by Croat (1997). In the Tropicos database Ramirez 1163 is a specimen of <i>Philodendron callosum</i> K. Krause.
<i>Cyclocephala santaritae</i> Ratcliffe, 1992a	<i>Attea insignis</i> (Mart.) Drude	COLOMBIA	Núñez-Avellaneda and Neita 2009	–
	<i>Oenocarpus</i> sp.	ECUADOR: Napo	Label data of H. Balslev and A. Henderson	Three voucher specimens examined from UNSM
<i>Cyclocephala sarpedon</i> Ratcliffe, 1992b	<i>Oenocarpus bacaba</i> Mart.	BRAZIL: Amazonas	Küchmeister <i>et al.</i> 1998	–
<i>Cyclocephala sexpunctata</i> Laporte, 1840 <i>incertae</i> <i>sedis</i> ( <i>Cyclocephala</i> morphospecies 1 <i>sensu</i> Moore 2011)	Araceae	GUATEMALA: Sololá (Las Tarrales Reserve); Huehuetenango (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 WICH. A single voucher examined from UVGC (Capistran).
	<i>Xanthosoma robustum</i> Schott	MEXICO: Chiapas (Cacahoatán); Guerrero (Mochitlán, Achauizolita)	Morón 1997; Label data of L. Delgado	A single voucher examined from UVGC. Morón (1997) reported this beetle as <i>C. sexpunctata</i> .
	<i>Xanthosoma sagittifolium</i> (L.) Schott	MEXICO: Chiapas (Cacahoatán)	Morón 1997	–
	<i>Xanthosoma</i> sp.	GUATEMALA: Quetzaltenango (El Palmar near Finca El Faro)	Label data of E. Cano	A single voucher examined from UVGC.
	<i>Xanthosoma wendlandii</i> (Schott) Standl.	MEXICO: Chiapas (Cacahoatán)	Morón 1997	–
<i>Cyclocephala sexpunctata</i> Laporte, 1840 <i>incertae</i> <i>sedis</i> ( <i>Cyclocephala</i> morphospecies 2 <i>sensu</i> Moore 2011)	<i>Alocasia macrorrhizos</i> (L.) G. Don	COSTA RICA: San José (Parque del Este)	Label data of uncredited collector; Valerio 1984	Eight voucher specimens examined from UNSM
	Araceae	PANAMA: Chiriquí (La Fortune, Quebrada Al Trail)	Label data of J. Ashe & A. Brooks	A single voucher examined from KSEM
	<i>Philodendron tripartitum</i> (Jacq.) Schott	COSTA RICA: San José (Parque del Este)	Label data of uncredited collector	Two vouchers examined from UNSM
	<i>Xanthosoma</i> sp.	COSTA RICA: Alajuela (San Ramon, Rio S. Lorencito)	Label data of A. Solís	A single voucher examined from INBC

**Appendix I.** Continued.

<i>Cyclocephala sexpunctata</i> Laporte, 1840 <i>incertae sedis</i> (ambiguous records)	<i>Philodendron grandipes</i> K. Krause	NO DATA	Croat 1997	–
	<i>Philodendron grayumii</i> Croat	PANAMA: Coclé (near El Copé)	Croat 1997	–
	<i>Philodendron sagittifolium</i> Liebm.	PANAMA: Panamá	Croat 1997	–
	<i>Philodendron solimoesense</i> A. C. Sm.	FRENCH GUIANA	Gibernau <i>et al.</i> 1999	–
	<i>Xanthosoma poeppigii</i> Schott	PERU: Loreto (Estación Biológica Madre Selva)	García-Robledo <i>et al.</i> 2005	–
	<i>Xanthosoma undipes</i> (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> Schott (García-Robledo <i>et al.</i> 2005, citing pers. comm. with T. Croat).
	<i>Xanthosoma wendlandii</i> (Schott) Standl.	COSTA RICA: Heredia (Santo Domingo); Alajuela (Alajuela)	Valerio 1988	–
<i>Cyclocephala simulatrix</i> Höhne, 1923	<i>Philodendron solimoesense</i> A. C. Sm.	FRENCH GUIANA	Ponchel 2006	–
	<i>Philodendron squamiferum</i> Poepp.	FRENCH GUIANA: Kourou	Gibernau and Barabé 2002	–
<i>Cyclocephala sparsa</i> Arrow, 1902	<i>Annona purpurea</i> Moç & Sessé ex Dunal	MEXICO: Michoacán	Murray 1993	–
	<i>Cymbopetalum baillonii</i> R. E. Fr.	MEXICO: Veracruz	Murray 1993	–
	<i>Cymbopetalum costaricense</i> (Donn. Sm.) R. E. Fr.	COSTA RICA: Heredia (La Selva Biological Station)	Schatz 1985	–
	<i>Cymbopetalum gracile</i> R. E. Fr.	MEXICO: Guerrero	Murray 1993	–
	<i>Cymbopetalum hintonii</i> Lundell	MEXICO: Jalisco	Murray 1993	–
	<i>Cymbopetalum torulosum</i> G. E. Schatz	COSTA RICA: Heredia (La Selva Biological Station)	Bawa <i>et al.</i> 1985a; Bawa <i>et al.</i> 1985b; Schatz 1985; Kress and Beach 1994	–
	<i>Malmea</i> aff. <i>depressa</i> (Baill.) R. E. Fr.	MEXICO: Veracruz (Estación Biológica Los Tuxtlas)	Schatz 1987	–



## Appendix I. Continued.

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

## Appendix I. Continued.

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



## Appendix I. Continued.

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



## Appendix I. Continued.

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

**Appendix I.** Continued.

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

**Appendix 1.** Continued.

Coleoptera	<i>Philodendron acuminatissimum</i> Engl.	NO DATA	Madison 1979	–
	<i>Philodendron cruentospathum</i> Madison	NO DATA	Madison 1979, citing pers. comm. from C. H. Dodson	Inflorescences of this plant species rotate to capture water after anthesis which is a strategy to drive beetles out of the spathe (Madison 1979).
	<i>Philodendron senatocarpium</i> 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).
	<i>Philodendron venosum</i> (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> (Grayum 1984).
	<i>Rhodospatha forgetii</i> 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).
	<i>Xanthosoma sagittifolium</i> (L.) Schott	NO DATA	Madison 1979	The plant species displays a “drowning” strategy similar to <i>Philodendron</i> (Madison 1979).
Evidence of beetle feeding	<i>Nymphaea oxypetala</i> Planch.	VENEZUELA	Wiersema 1987	–

**Appendix 2.** Cyclocephaline synonyms reported in the floral association literature.

Valid Name	Synonym (Reported Name)	Reference
<i>Cyclocephala amazona</i> (Linnaeus, 1767)	<i>Cyclocephala signata</i> (Fabricius, 1781)	Mora-Urpí and Solís 1980; Mora-Urpí 1982; Gottsberger 1986
<i>Cyclocephala brevis</i> Höhne, 1847	<i>Cyclocephala pubescens</i> Burmeister, 1847	Valerio 1984; Valerio 1988
<i>Cyclocephala epistomalis</i> Bates, 1888	<i>Cyclocephala mollis</i> Endrödi, 1963	Prance 1980
<i>Cyclocephala maffafa</i> Burmeister, 1847	<i>Cyclocephala maffafa</i> [sic] <i>grandis</i> Burmeister, 1847	Ponchel 2006
<i>Cyclocephala melanocephala</i> (Fabricius, 1775)	<i>Cyclocephala dimidiata</i> Burmeister, 1847 <i>Dichromia dimidiata</i> (Burmeister, 1847)	Cockerell 1897; Moore 1937; Saylor 1945; Linsley 1960



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

Valid Name	Synonym (Reported Name)	Reference
<i>Annona warmingiana</i> Mello-Silva & Pirani	<i>Annona pygmaea</i> (Warm.) Warm.	Gottsberger 1986; Gottsberger 1989
<i>Astrocaryum aculeatissimum</i> (Schott) Burret	<i>Astrocaryum arii</i> Mart.	Luederwalt 1926
<i>Attalea speciosa</i> Mart.	<i>Orbignya phalerata</i> Mart.	Anderson <i>et al.</i> 1988
<i>Attalea spectabilis</i> Mart.	<i>Orbignya spectabilis</i> (Mart.) Burret	Küchmeister <i>et al.</i> 1993
<i>Bactris coloradonis</i> L. H. Bailey	<i>Bactris porschiana</i> Burret	Beach 1984; Ratcliffe 2003
<i>Bactris hirta</i> var. <i>pectinata</i> (Mart.) Govaerts	<i>Bactris hirta</i> var. <i>spruceana</i> (Trail) A.J.Hend.	Henderson <i>et al.</i> 2000
<i>Bactris hondurensis</i> Standl.	<i>Bactris wendlandiana</i> Burret	Bullock 1981; Ratcliffe 1992a
<i>Bactris maraja</i> Mart.	<i>Bactris monticola</i> Barb. Rodr.	Listabarth 1996
<i>Brugmansia</i> sp.	<i>Datura arborea</i> (no author)	Ohaus 1910; Gottsberger 1986
<i>Cryosophila williamsii</i> P. H. Allen	<i>Cryosophila albida</i> Bartlett	Henderson 1984; Silberbauer-Gottsberger 1990
<i>Datura innoxia</i> Mill.	<i>Datura meteloides</i> DC. ex Dunal	Cockerell 1897
<i>Lecythis lurida</i> (Miers) S. A. Mori	<i>Holopyxidium jaranum</i> Huber ex Ducke	Prance 1976
<i>Mandevilla longiflora</i> (Desf.) Pichon	<i>Macrosiphonia longiflora</i> (Desf.) Müll. Arg.	Gottsberger 1986
<i>Magnolia ovata</i> (A. St.-Hil.) Spreng.	<i>Talauma ovata</i> A. St.-Hil, 1824	Gibbs <i>et al.</i> 1977; Gottsberger 1986; Gottsberger 1989
<i>Oenocarpus</i> sp.	<i>Jessenia</i> sp.	Label data of Balslev and Henderson. Three specimens deposited in UNSM
<i>Nymphaea glandulifera</i> Rodschied	<i>Nymphaea blanda</i> var. <i>fenzliana</i> (Lehm.) Casp.	Cramer <i>et al.</i> 1975
<i>Philodendron bipinnatifidum</i> Schott ex Endl.	<i>Philodendron selloum</i> C. Koch	Gottsberger 1986; Gottsberger and Amaral 1984; Gottsberger and Silberbauer-Gottsberger 1991
<i>Philodendron venosum</i> (Willd. ex Schult. & Schult.f.) Croat	<i>Philodendron karstenianum</i> Schott	Grayum 1984
<i>Phytelephas aequatorialis</i> Spruce	<i>Palandra aequatorialis</i> (Spruce) O. F. Cook	Balslev and Henderson 1987
<i>Tabernaemontana</i> sp.	<i>Peschiera</i> sp.	Gottsberger 1986
<i>Victoria amazonica</i> (Poepp.) J. C. Sowerby	<i>Victoria regia</i> Lindl.	von Bayern 1897; Knuth <i>et al.</i> 1904; Gessner 1962; Martínez 1968
<i>Xanthosoma mexicanum</i> Liebm.	<i>Xanthosoma pilosum</i> K. Koch & Augustin	Beath 1998
<i>Xanthosoma sagittifolium</i> (L.) Schott	<i>Xanthosoma violaceum</i> Schott	Morón 1997
<i>Xanthosoma striatipes</i> (Kunth & C. D. Bouché) Madison	<i>Caladium striatipes</i> (Kunth & C. D. Bouché) Schott	Schrottky 1910; Gottsberger 1986; Gottsberger 1989
<i>Xanthosoma wendlandii</i> (Schott) Standl.	<i>Xanthosoma hoffmanni</i> [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
<i>Alocasia macrorrhizos</i> (L.) G. Don (pers. comm. with T. B. Croat, May 2011)	<i>Xanthosoma macrorrhizas</i>	Valerio 1984; Label data of unaccredited collector
<i>Dieffenbachia tonduzii</i> Croat & Grayum (pers. comm. with T. B. Croat and M. Grayum, May 2011)	<i>Dieffenbachia longivaginata</i> Croat & Grayum <i>ined.*</i>	Label data of M. Grayum. Beetle voucher specimens deposited at INBC
<i>Philodendron ligulatum</i> Schott (pers. comm. with T. B. Croat and M. Grayum, May 2011)	<i>Philodendron atlanticum</i> Croat & Grayum	Grayum 1984; Label data of H. Young
<i>Philodendron ptarianum</i> Stey. or <i>Philodendron rugosum</i> Bogner & G.S.Bunting	<i>Philodendron ptarianum</i> Stey. var. <i>rugosum</i> Bunt.	Ramírez 1989; Ramirez 1992
Unresolved	<i>Cereus perambucensis</i> Lem.	Rosa <i>et al.</i> 1995; Rosa <i>et al.</i> 1999; Lechance <i>et al.</i> 2001
Unresolved	<i>Kielmeyera variabilis</i> Mart. & Zucc.	Gottsberger 1986
Unresolved	<i>Malmea manausensis</i> Maas & Miralha	Gottsberger <i>et al.</i> 1998

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