

# Soapberry Bug (Hemiptera: Rhopalidae: Serinethinae) Native and Introduced Host Plants: Biogeographic Background of Anthropogenic Evolution

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**ABSTRACT** Soapberry bugs (Hemiptera: Rhopalidae: Serinethinae) have recently colonized introduced and invasive plants in the soapberry family (Sapindaceae), and they have rapidly differentiated as a result. These plants have been carried among continents at many places and times, and they may possess alien coevolutionary histories with other soapberry bug genera and species, exposing native bugs worldwide to both new challenges and new opportunities in host exploitation. To provide geographic and phylogenetic contexts for this human-catalyzed evolution, we analyzed the worldwide host relations of the three soapberry bug genera on native versus non-native sapinds. We found that the adopted introduced hosts are taxonomically distant from native hosts in six of seven global biogeographic regions. Only a few genera account for most of the introductions, and natives and non-natives are now reciprocally distributed across several pairs of continents. The evolutionary result may be local diversification, but also global convergence on currently rare bug phenotypes when plants with small endemic ranges are widely exported.

**KEY WORDS** *Boisea*, invasion, *Jadera*, *Leptocoris*, Sapindaceae

The relationship between human-caused environmental change and the responses of populations in nature is not simple. Maladaptive individual responses may increase mortality, decrease natality, and contribute to extinctions (Schlaepfer et al. 2005). Alternatively, adaptive phenotypic plasticity and evolution may improve persistence (Ghalambor et al. 2007, Kinison and Hairston 2007, Carroll and Watters 2008). Changed phenotypes will frame how populations interact with both new and old elements of their environments (Palumbi 2001, Strauss et al. 2006, Carroll 2011). One consequence of anthropogenic evolution may be population differentiation and biodiversification, although little is known about this phenomenon.

Among human impacts on biotic systems, species introductions are of central importance (e.g., Crowl et al. 2008), in part because of the power of invasive populations to grow and spread without further human assistance. Alien species may cause selection in native species by acting as predators, parasites, competitors, traps, or resources (Strauss et al. 2006, Strayer et al. 2006). Because evolution in response to novel selection pressures should be more likely in growing than in declining populations (e.g., Reznick and Ghalambor 2001), adaptation by natives to novel species may be especially likely when those novel species are

beneficial to them rather than antagonistic (e.g., Carroll 2008).

Soapberry bugs (Hemiptera: Rhopalidae: Serinethinae) are good examples of these processes. These insects consist of  $\approx 65$  species (Göllner-Scheiding 1982) of seed predators specialized on plants in the “soapberry” family, or Sapindaceae. On multiple continents, they have adopted introduced plants of the soapberry family as hosts (Carroll and Loye 1987, Carroll et al. 2005b). The two species of soapberry bugs that have been studied in ecological detail show rapid, complex, repeating, and reversing adaptive evolution after their adoption of introduced sapinds in recent decades (*Jadera haematoloma* Herrich-Schaeffer and *Leptocoris tagalicus* Hahn; Carroll et al. 1997, 1998, 2005a; Dingle et al. 2009). Cross-rearing experiments indicate that their developmental and reproductive adaptations to introduced host plants have evolved at a steep cost to their performance on the native host plants used by their recent ancestors. Most performance changes are genetically controlled, and they involve genes of major effect (Carroll 2007, 2008).

The purpose of this paper is to place the ongoing adaptive diversification of the soapberry bugs in its historical biogeographic context. Despite their ecological prominence on most continents (outside of Europe, northern Asia, and Antarctica; Fig. 1), no synthesis of the natural history of the Serinethine rhopalids has been published. As in the better-known soapberry bug species, similar eco-evolutionary re-

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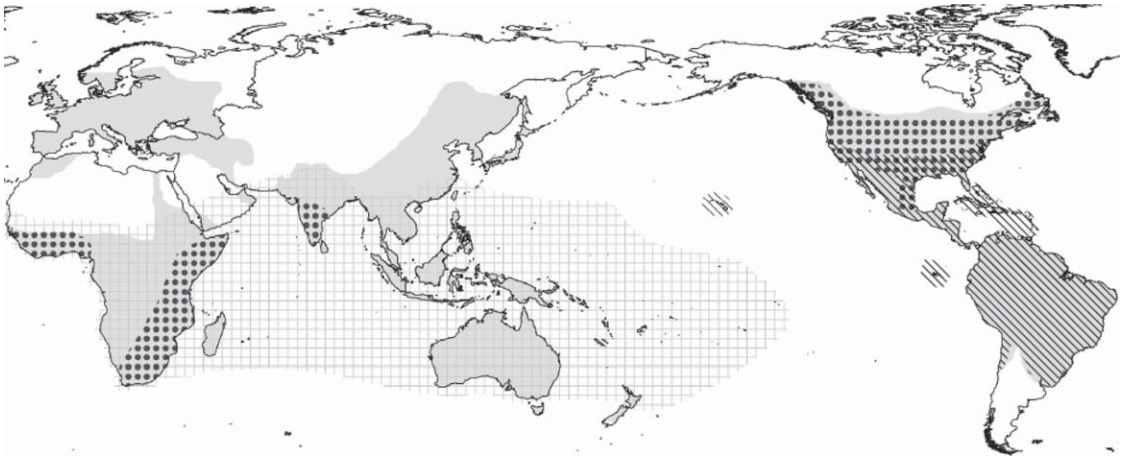


Fig. 1. World geographic distributions of the soapberry bugs and the host plant family Sapindaceae. Legend: gray, Sapindaceae; grid pattern, bug genus *Leptocoris*; dots, bug genus *Boisea*; and diagonal lines, bug genus *Jadera*.

sponses may be taking place in many others that are also feeding on novel hosts. In each case, assigning native versus ancestral host affiliations is the first step for evolutionary analysis, but there is scarce published information on host relations. Do the three soapberry bug genera differ in the native host taxa they exploit, and among soapberry plant tribes in the degree to which the bugs exploit them? Do phylogenetic constraints and capacities influence the taxa the insects adopt? Are introduced sapinds from a phylogenetically broad or narrow set of species, and how closely are they related to the native sapinds in communities into which they have been introduced? Are there parallels between contemporary host-based diversification and deeper phylogenetic patterns of association? Addressing these questions will help to root contemporary eco-evolutionary findings within the context of the deeper ancestral relations between soapberry bugs and the Sapindaceae.

We present data on the host associations of 16 of the 42 described *Leptocoris* Hahn, nine of the 17 *Jadera* Stål, and all four *Boisea* Kirkaldy species. Most of the data on host associations are published here for the first time, and their taxonomic consistency supports our use of the common name “soapberry bugs” for the entire rhopalid subfamily Serinethinae. This taxonomy of host relations serves as a basis for understanding both historical and contemporary aspects of these insects’ host-centered evolution and provides a practical starting point for studies of their biotic interactions around the world. Range maps for the insect species considered here are presented at [www.soapberrybug.org](http://www.soapberrybug.org).

### Materials and Methods

**Study Organisms.** Soapberries, or sapinds, consist of  $\approx 1,900$  species in 150 genera of tropical and subtropical trees, shrubs, and vines in four subfamilies (Buerki et al. 2009, Acevedo-Rodríguez et al. 2011) (Fig. 1). They include plants cultivated for fruit, oil, stimulant,

and ornamental values; timber trees; and agricultural and environmental weeds. The family is ecologically prominent in low- to mid-latitude continental regions as well as on Pacific Islands (Acevedo-Rodríguez et al. 2011). Through their relationship to the sapinds, soapberry bugs are important to economies, ecology, and conservation worldwide (Carroll et al. 2005a,b; Carroll 2008).

Soapberry bugs are relatively large (8–30 mm) and approachable true bugs that are often brightly colored (Göllner-Scheiding 1983, Carroll and Loye 1987). They are mainly tropical and subtropical, occurring within the range of the Sapindaceae (Fig. 1; Table 1), the seeds of which they depend on for development and reproduction. *Leptocoris* is the most broadly distributed genus. It occurs from sub-Saharan Africa through Asia and Australia to the Pacific. *Jadera* occurs in North and South America and was accidentally introduced to Hawaii in the 1960s (Gagné 1971). Soapberry bugs have not colonized Europe or apparently temperate Asia, despite the fact that the maples (*Acer*, *Dipteronia*) are present. In contrast, two endemic *Boisea* (“box elder bugs”) have colonized maples to mid-latitudes in North America. The other two *Boisea* species are in Asia and Africa, respectively.

Five publications have treated these insects’ host associations. Based on a slim extant literature, Schaefer and Chopra (1982) and Schaefer and Mitchell (1983) first reported a relation between serinethines and the rosid order Sapindales. Carroll and Loye (1987) presented records for five of the New World genus *Jadera*, mainly regarding sapinds on which they observed feeding by juveniles and reproductive adults. They also discounted a reference to *Jadera* on Moraceae. Similarly, Carroll et al. (2005a) reported sapindaceous hosts for the five *Leptocoris* species in Australia and discounted a reference to Rutaceae. In a paper not seen by those authors, Göllner-Scheiding (1997) lists some plant records without inclusion criteria but provides a clear sapind host record (see *Appendix*), albeit misassigned to Rutaceae.

**Table 1.** Geographic distributions of the three soapberry bug genera *Leptocoris*, *Jadera*, and *Boisea*, with number of species and endemic species for each genus within each designated region

Genus	Total species	Africa <sup>a</sup>	Asia <sup>b</sup>	Australia	Pacific Islands <sup>c</sup>	North and Central America <sup>d</sup>	South America
<i>Leptocoris</i>	42	21/21	13/7	5/1	11/5	0	0
<i>Jadera</i>	17	0	0	0	1/0 <sup>e</sup>	8/4	13/9
<i>Boisea</i>	4	1/1	1/1	0	0	2/2	0

Based on Göllner-Scheiding (1983) and Gross (1960).

<sup>a</sup> Including Madagascar.

<sup>b</sup> Asia includes the continent and adjacent islands, including islands of the Indian Ocean east of Madagascar, and Indonesia as far east as Bali and Borneo.

<sup>c</sup> Pacific Islands region includes Wallacea, Philippines, Melanesia, Micronesia, Polynesia, and Hawaii.

<sup>d</sup> Canada to Panama, and including Islands of the Gulf of Mexico and Caribbean south through the Lesser Antilles.

<sup>e</sup> A mainland American species, *J. haematoloma*, was introduced to Hawaii in the 1960s. See text for details.

Eliminating the misleading records and attribution has helped to bring the focus squarely on Sapindaceae.

**Data Sources and Their Use.** To characterize host relations, we mined information from published sources, from specimen labels in museums with global collections as well as in regional museums near sites of fieldwork, and from the fieldwork itself. Well-documented unpublished data of other naturalists also contribute to the data set.

Museum records also supported field studies in two ways. First, we traveled to sites of insect collections in search of hosts. Collections of nymphs or brachypterous adults were especially valuable for this support, because they pointed directly to (historical) host locales. Second, from herbarium records, we traveled to sites at which certain plant species had been collected to evaluate their status as hosts by searching for bugs. Herbarium specimens likewise provided information on fruiting phenology, allowing us to conduct fieldwork at appropriate seasons.

For observations in nature, “host” refers to a plant on which Serinethines were observed feeding and mating, or at which nymphs were present (with the few exceptions noted above, and when no other potential host species were within obvious walking distance for a nymph [ $\approx 500$  m]). Accepted literature records are based on similar criteria. For museum specimens, notes on plant associations were rare (<1%), with sapind records constituting the majority. From among these, we rejected records of sapinds commercially cultivated for fruit (e.g., lychee, longan, and rambutan), from which insects are probably more likely to be sampled, and from whose fruit these insects drink, but for which we have no definitive records of seed feeding or reproduction. [Excluded as a result are records for *Leptocoris isolatus* Distant and *L. tagalicus* in Australia, and *Boisea fulcrata* (Germar) in South Africa, despite that fact that these Australian records were accepted under the more inclusive criteria of Carroll et al. 2005b.] On similar grounds, we also rejected museum records tagging common native or agricultural plants as hosts. Records of sap and nectar feeding for nonreproductive maintenance (Wolda and Tanaka 1987) also were excluded. Lastly, we searched more extensively and intensively for hosts in North America and Australia than elsewhere.

**Taxonomy of Insects and Plants.** Insect identifications were based on Gross (1960) and Göllner-Schei-

ding (1979, 1980, 1982, 1983) and on comparisons of field collections to type specimens. For plant identification, we used herbarium specimens as regional references (Croat 1978, Tomlinson 1980, Reynolds 1985, Davies and Verdcourt 1998).

The higher classification of Sapindaceae has recently been revised by Buerki et al. (2009, 2010) based mainly on new molecular data. We follow their subfamilial and “group” assignments but retain traditional tribal nomenclature for these groups, rather than the authors’ temporary genus-based group names. We also exclude genus *Xanthocerus* from the soapberries (Buerki et al. 2010), but we do not follow their suggestion that the maple subfamily be excluded.

**Organization of Data Tables and Definition of Terms.** Data are tabulated by host taxonomy, insect genus, and geographic realm, in combinations that address particular aspects of native and non-native biotic associations.

We define “native” hosts as those that occur naturally in the wild in the habitat in which a host association was observed. A minority of native records is for planted taxa that are listed as native in regional floras (e.g., in botanical gardens). “Introduced” hosts include both naturalized and planted individuals, generally transported between global biogeographic regions. However, in a few cases this designation also includes plants native to a country but not to the locale of collection. These involve plants transported hundreds of kilometers from native ranges in which they are not hosts to soapberry bugs.

## Results

### Bug–Host Relations

Of the three soapberry subfamilies, members of Hippocastanoideae and Sapindoideae were found to be hosts, whereas members of Dodonaeoideae were not. Table 2 presents Old and New World native host relations at the tribal level by bug genus and geographic realm. Table 3 then compares use of native versus introduced sapind tribes by each bug genus. Associations of individual soapberry bug and sapind species around the world are detailed in the *Appendix*.

***Leptocoris*.** The largest genus, *Leptocoris*, consists of 42 described Paleotropical–subtropical species (Table 1). It is found on native taxa in six of the 12 sapindoid

**Table 2.** Subfamilies and tribes of Sapindaceae recognized in this paper, with their native geographic distributions, and the genera of associated soapberry bug seed predators on native host plants

Subfamily	Tribe	Old World		New World	
		Region	Predators	Region	Predators
Hippocastanoideae	Acereae	Eurasia, North Africa		North America	<i>Boisea</i>
	Hippocastaneae	Eurasia		North and South America	
Dodonaeoideae	Doratoxyleae	Paleotropics		Neotropics	
	Dodonaeeae	Paleotropics		Neotropics	
Sapindoideae	Delavayaeae	South China		North America	
	Koelreuterieae	East and South-East Asia	<i>Leptocoris</i>		
	Schleicherieae	India, SE Asia	<i>Leptocoris</i>		
	Nephelieae	Paleotropics			
	Sapindeae	Paleotropics	<i>L. &amp; Boisea</i>	North & South America	<i>Jadera</i>
	Macphersonieae	Africa	<i>Boisea</i>		
	Cupanieae	Paleotropics	<i>Leptocoris</i>		
	Tristropsiseae	Oceania			
	Blomieae	Africa		Neotropics	
	Melicocceae			Neotropics	
	Thouinieae	Paleotropics	<i>Leptocoris</i>	Neotropics	<i>Jadera</i>
Paullinieae	Africa	<i>Leptocoris</i>	Neotropics	<i>Jadera</i>	

See Table 3 and the *Appendix* for records on introduced plants.

tribes (Table 2). *Leptocoris* species frequently colonize introduced sapinds, including those from the Americas, but we have just a single indication of colonization of the other host subfamily, Hippocastanoideae, which is otherwise used only in North America (Table 3; *Appendix*).

*Africa: Native Hosts in Tribes Paullinieae and Thouinieae.* Approximately half of *Leptocoris* species are African endemics (including Madagascar; Table 1). Host data are for eight species from Namibia, South Africa, Ghana, Tanzania, and Uganda. Native hosts are in both Thouinieae and Paullinieae, whereas introduced hosts are only in Paullinieae. *Allophylus* species, widespread in mesic sub-Saharan Africa (Davies and Verdcourt 1998), are common hosts in South Africa and Zanzibar. Native and introduced vines of the genus *Cardiospermum* species are also commonly used. *Paullinia* is a highly speciose genus of vining hosts in the Neotropics (see below), has it but one Paleotropical species, and it is used by at least one African *Leptocoris* (museum record, Ghana).

*Asia: Native Hosts in Tribes Paullinieae, Thouinieae, Schleicherieae, and Koelreuterieae.* We have host information for just four of the 13 Asian *Leptocoris* species recognized by Göllner-Scheiding (1980, 1982). Records are from India, China, Malaysia, Taiwan, and Japan, and they are most comprehensive for Taiwan and Japan. Tribal relations with native sapinds seem more various in Asia than in Africa. All listed Asian bug species have immense geographic ranges. *L. augur* is the best studied, being common on the vining Neotropical invader *Cardiospermum halicacabum* L. (Paullinieae) as well as the economically valuable lac tree [*Schleichera oleosa* (Lour.); Schleicherieae]. *C. halicacabum* accounts for seven of the 16 Asian records. *Leptocoris vicinus* (Dallas) is the native seed predator of the endemic tree *Koelreuteria elegans* subsp. *formosana* Laxm. (Koelreuterieae), which is in turn a commonly colonized horticultural introduction in several subtropical regions. In adjacent southern Japan, *L. vicinus* instead uses the introduced *C. halicacabum*.

**Table 3.** Native versus introduced hosts: subfamilial and tribal relationships by bug genus and geographic region

Genus	Region	Native host subfamilies	Native host tribes	Introduced host subfamilies	Introduced host tribes
<i>Leptocoris</i>	Africa	Sapindoideae	Paullinieae Thouinieae	Sapindoideae	Paullinieae
	Asia	Sapindoideae	Schleicherieae Thouinieae Koelreuterieae	Sapindoideae	Paullinieae
	Australia	Sapindoideae	Cupanieae Thouinieae Sapindeae	Sapindoideae	Paullinieae Schleicherieae Koelreuterieae
<i>Jadera</i>	Pacific Islands	Sapindoideae	Thouinieae	Sapindoideae	Nephelieae
	North America	Sapindoideae	Paullinieae Sapindeae	Sapindoideae	Koelreuterieae Sapindeae
	Central America South America	Sapindoideae Sapindoideae	Paullinieae Paullinieae Thouinieae		
<i>Boisea</i>	Africa	Sapindoideae	Macphersonieae	Hippocastanoideae	Acereae
	Asia	Sapindoideae	Sapindeae		
	North America	Hippocastanoideae Sapindoideae	Acereae Sapindeae	Hippocastanoideae Sapindoideae	Acereae Koelreuterieae

*Australia: Native Hosts Mainly in Tribe Cupanieae; also Sapindeae, Paullinieae, and Thouinieae.* Four of the five Australian bug species are represented, distributed among 16 hosts, many of which are confined to the warmer and wetter habitats of the east and north. In most areas, endemic members of the genus *Alectryon* are common hosts (Cupanieae; Carroll et al., 2005a). *L. tagalicus*, which ranges widely in and beyond Australia, uses at least 14 host species here, two of which are introduced. In addition to native *Alectryon* (and related *Ellatostachys*), it also uses widespread native *Atalaya* species (Sapindeae) and rare tropical northern *Allophylus* (Thouinieae).

Endemic *L. mitellatus* is likewise polyphagous but less frequent and common than *L. tagalicus* on non-native hosts in subtropical latitudes (Carroll et al. 2005a). It is the sole known Australian seed predator on introduced Asian *Koelreuteria paniculata* Lxm. (South Australia). *L. rufomarginatus*, which depends mainly on *Alectryon* and *Ellatostachys* in the east, occurs on native *A. cobbe* in tropical coastal Northern Territory. *L. vicinus* is restricted to plantings of the Asian tree *Schleichera oleosa* Lour. around Darwin in the Northern Territory and may be an accidental human introduction. The substantial diversity of fruiting Australian sapinds on which *Leptocoris* has not been observed include species of *Dodonea* as well as many genera in Cupanieae.

*Pacific: Native Hosts in Tribe Thouinieae.* The native Pacific *Leptocoris* exhibit two types of geographic associations. First are island endemics (e.g., the namesake *L. marquesensis*, as well as *L. fuscus* and *L. miniscula* of Timor). Second are a few far-flung species, often with ranges that match those of *Allophylus* host species. Bird-dispersed seeds (Leenhouts 1994) may promote island-hopping by hosts, which are then tracked down by volant bugs. *L. isolatus* is on *Allophylus* from New Guinea to the Marshall Islands; *L. rufomarginatus* is on *Allophylus* from northern Australia to the Caroline Islands and to southern Japan. *Pometia*, or Pacific lychee (Nephelieae), used by *L. insularis* in the Tuatamotu Archipelago of French Polynesia, represents the easternmost Pacific predation record. Preindustrial Polynesians may have transported that host eastward.

*Jadera.* We have host records for nine of the 17 species of *Jadera*, on three of the five native New World tribes of the sapindoid subfamily. Almost all *Jadera* are predators of tribe Paullinieae, especially *Cardiospermum*, *Serjania*, and *Paullinia*. Two species in other tribes also are used: tropical *Allophylus edulis* in the Thouinieae and the temperate variety of *Sapindus saponaria* in the Sapindeae. None of the other sapindoid tribes are known to be hosts, including members of the native Neotropical Melicocceae and proposed Blomieae tribes.

*North America (Including Canada, United States with Hawaii, Bahamas, and Mexico).* Native hosts mainly in tribe Paullinieae, also Sapindeae. Of the five *Jadera* species that extend north of Mexico, only *J. haematoloma* inhabits temperate environments. It uses at least 11 host taxa and is adaptively differentiated

among both native and introduced hosts (e.g., Carroll 2007). In addition to using vines of Paullinieae, populations in the south central and southwestern United States use *Sapindus* (Sapindeae). Native *Sapindus* taxa in subtropical southern Florida and Texas (and elsewhere through the Neotropics) seem not to be used. All three species of East Asian *Koelreuteria* (Koelreuterieae) are also hosts of *J. haematoloma*. Furthermore, this insect was inadvertently introduced to Hawaii (apparently in the 1960s) and quickly colonized several native and introduced sapinds, including two native *Sapindus* species and introduced *Cardiospermum* and *Koelreuteria* (Carroll and Loye 1987).

Vines of Paullinieae (*Cardiospermum*, *Paullinia*, *Serjania*, and *Urvillea*) are together the native hosts of the other four North American *Jadera* species for which we have records. At least three other sapinds native to the southernmost United States are not hosts: *Exothea*, *Hypolate*, and *Ungnadia* (S.P.C. and J.E.L., unpublished data).

*Central America: Native Hosts in Tribe Paullinieae.* Hosts are four genera of mainly large native vines in Paullinieae, including *C. grandiflorum*, which is an environmental weed colonized by native soapberry bugs in Australia, South Africa, Hawaii, California, and perhaps Raratonga.

*South America (Including Galapagos and Fernando Noronha): Native Hosts in Tribes Paullinieae and Thouinieae.* The 500 species of Neotropical sapind lianas (including *Cardiospermum*, *Paullinia*, *Serjania*, *Thinnouia*, and *Urvillea*) account for 60% of regional family diversity and >25% of the world diversity (Acevedo-Rodríguez et al. 2011). *Jadera* is more diverse here than in North America, and we have host records for five of the 14 recorded species. Two are on *Cardiospermum*, one on *Serjania*, and two on *Allophylus* (Thouinieae).

*Boisea.* This genus was split from *Leptocoris* by Göllner-Scheiding (1982) based on morphological differences. The resulting geographic distribution is broad but disjunct: one species is widespread in Africa, one in India, and two in North America. We have host records for all of them.

*Africa: Native Hosts in Tribe Macphersonieae.* The widespread and occasionally planted native fruit tree *Pappea capensis* (Macphersonieae) supports seasonally large populations of *B. fulcrata* in far southern Africa. We lack host records for this insect in other regions of Africa, but note that the geographic range of *P. capensis* in southern and eastern Africa largely matches that of the eastern subspecies *B. f. fulcrata* (Fig. 1). Hankey's (2004) attribution of *P. capensis* as host to *L. hexophthalmus* requires verification because that name has been consistently misapplied to *B. fulcrata* (Göllner-Scheiding 1980). From a museum specimen, Göllner-Scheiding (1980) reported the native fruit tree *Blighia umijugatus* Baker (Nephelieae) as a host of *B. flava* in West Africa (later synonymized with *B. fulcrata* as subspecies *flava* by the same author in 1982). *B. f. fulcrata* has been collected in numbers on *Blighia*'s horticultural relative *Litchi chinensis* Somm. in South Africa, although at present we reject these as

evidence of a host association with these members of Nephelieae for the reasons specified in Materials and Methods.

As in adjacent Eurasia, we found no indication that maples (*Acer*) are used where native in northwestern Africa. However, one South African collection of five adults suggests colonization of East Asian *Acer buergerianum* Miq., a commonly planted street tree in tribe Acereae.

*Asia: Native Host in Tribe Sapindeae.* *B. coimbatorensis* is shown from two Indian records to use native *Sapindus*.

*North America: Native Hosts in Tribes Acereae and Sapindeae.* Two species of *Boisea* occur here. One species is in the southwest and far west [*Boisea rubrolineata* (Barber)] of the United States and Canada, and the other mainly farther east [*Boisea trivitatta* (Say)], having spread eastward from the west central United States in the last century (Smith and Shepherd 1937, Slater and Schaefer 1963), and also in eastern Mexico. These are the "box elder bugs," named for their widespread maple host "box elder" (*Acer negundo* L., tribe Acereae).

Like *Jadera* in North America, *Boisea* use a range of native and introduced hosts. *B. rubrolineata* has adopted Asian *Koelreuteria* spp. in northern California. *B. trivitatta*, in addition using native boxelder (*A. negundo*) also occurs on native *Sapindus* in a limited area of northern Arizona. Despite range expansion onto eastern populations of *A. negundo* within diverse communities of native *Acer* species, it has not colonized other *Acers* there other than *Acer saccharinum* L. It also has adopted *A. saccharinum* cultivated in Oklahoma, to the west of that plant's native range, and *Acer grandidentatum* Nutt. in Texas, to the east of that plant's native range. Within its new eastern U.S. range, it has however adopted the East Asian maples *Acer ginnala* Maxim. and *A. buergerianum* (the latter being the same maple species attracting its congener *B. fulcrata* in South Africa).

#### Use of Native and Introduced Hosts

At higher taxonomic levels, there is clear geographic structure to the distribution of native versus introduced host taxa (Table 3). In six of the seven global biogeographic regions in which introduced sapinds have been colonized, some or all of the introduced hosts are in tribes absent from the native flora. Present knowledge indicates that among global regions, Australia has been particularly subjected to colonization by phylogenetically distant sapinds that have nevertheless been colonized by native soapberry bugs.

Most prominent among the introduced tribes are the Neotropical Paullinieae, owing to *Cardiospermum* vines, and East Asian Koelreuterieae, owing to the ornamental *Koelreuteria* trees. These genera are now important agricultural and environmental weeds (Carroll et al. 2005c). Genus *Cardiospermum* vines host at least eight Paleotropical and five Neotropical bug species, and the global weed *C. halicacabum* alone

hosts at least 10 bug species and accounts for half of all Asian host records. In comparison, among native host plants, the arborescent, pantropical *Allophylus* species support the greatest diversity of soapberry bug seed predators, hosting at least seven Paleotropical and two Neotropical species.

#### Discussion

An important challenge for entomologists and other biologists is to understand how organisms are responding to global change. Measuring change requires describing the initial conditions, and this paper's list of the native host plants of soapberry bugs lays groundwork for investigating their preindustrial host adaptation. Tabulating these insects' non-native hosts then reveals that they have colonized a relatively small phylogenetic subset of sapinds that have been transported intercontinentally. These introduced hosts have been sufficiently closely related to the insects' native hosts to permit colonization, but sufficiently distantly related to select for rapid multitrait evolution, thus setting the stage for their recent and ongoing adaptation to these human-caused plant introductions.

Plant subfamily strongly structures the host associations. Of the three sapind subfamilies, only the sapindoid taxa are widely exploited. In contrast, just a few species of Nearctic hippocastanoid maples also are used where native, and we have no evidence for use of the diverse Dodonaeoideae, nor of the closely related monotypic family Xanthoceraceae, which was split from Sapindaceae by Buerki et al. (2010). This leaves the relationships within the Sapindoideae as being of particular interest.

Paleotropical *Leptocoris* uses six of 12 native sapindoid tribes, and New World *Jadera*, just three, nested within those *Leptocoris* uses (Table 2). The tribes that *Leptocoris* attacks (Paullinieae, Thouinieae, Schleicherieae, Koelreuterieae, Cupanieae, and Sapindeae) are seemingly scattered throughout sapindoid phylogeny (Buerki et al. 2009). *Jadera* is restricted to North and South America, and the Neotropics support only about half of the host tribal diversity present in the Paleotropics (Table 1). Neotropical sapind generic diversity and generic endemism are comparable to Africa but depauperate in comparison to the Indomalasian floristic subkingdom (Nianhe and Xianrui 1995). At the same time, the tribes that *Jadera* uses—Sapindeae, Thouinieae, and Paullinieae—are more diverse in the Neotropics (Nianhe and Xianrui 1995). Neotropical vines of the Paullinieae alone constitute >25% of the entire family species diversity, and it is with these phylogenetically recent (Harrington et al. 2005; Buerki et al. 2009) taxa that *Jadera* is most strongly associated. Fossil pollen of *Cardiospermum*, *Serjania*, and *Paullinia* place them in strata as early as upper-Eocene Panama (Graham 1985), but the insect's deeper history is not known.

*Boisea* is qualitatively quite different. It is the only genus to use maples (*Acer*, subfamily Hippocastanoideae) and it also uses two sapindoid tribes as

native hosts. Göllner-Scheiding (1982) suggests that these insects' low diversity but global distribution reflects a relictual status, and this interpretation seems consistent with its geographically partitioned use of taxonomically disparate hosts.

The historical biogeography of the Sapindaceae strongly influences the relative relatedness between native and introduced sapinds. In addition to *Litchi* and related fruit trees in the Nephelieae (attractive to soapberry bugs but not generally confirmed as hosts), the commonly imported horticultural sapinds are mainly flowering trees of the Koelreuterieae and vines of the Paullinieae. These host taxa, recently made global, originated from discrete regions, and they are often genetically and phenotypically distant from the native host taxa they join, creating as a result sudden and severe contemporary perturbations in the local adaptive landscapes (Table 3). The degree and form of alien plant differences from natives probably influence both the probability that native bugs will colonize them (*sensu* Agrawal et al. 2006), and the direction and rate of adaptation to them (Carroll 2008). Trait differences between native and adopted alien sapinds have selected not only for differences in beak length but also in developmental and reproductive performance, host preference, life-history organization, and flight polymorphism frequencies (Carroll and Boyd 1992; Carroll et al. 1997, 1998, 2005a).

The insects' rapid multitrait evolution shows limitations in their preadaptation to specific novel host species, despite being attracted to feed on them. The pertinent selective differences among native and introduced hosts are products of deeper phylogenetic divergence among host clades (in many cases including historical interactions with native soapberry bugs within the plants' native ranges). In some cases, it may be the relative abundance of uncontested seeds on non-native hosts that permits poorly adapted colonist bugs to persevere through what would otherwise become a major fitness deficit. In fact we do not know for certain that all host records herein represent successful colonizations, rather than records of "trapped" individuals whose lineages will not ultimately persist on a particular host. In contrast, alien hosts closely related to native hosts may require relatively simpler or less extensive genetic changes, relying, e.g., on standing additive genetic variation. As our baseline, we do know that adaptive evolution to Old World Koelreuterieae in ancestrally Paullinieae-dependent Florida bugs has required much more: complex epistatic differentiation in addition to additive genetic change (Carroll 2007).

At the same time, cases in which bugs have colonized introduced hosts that are either congeneric or conspecific with regional natives that they avoid (e.g., *J. haematoloma* on *Sapindus mukorossi* Willd. in Florida, where they eschew the native *Sapindus saponaria* L., and *Boisea trivittata* on novel *Acer* species in Texas and Oklahoma; Appendix) suggest that local history plays a strong role in host choice and adaptation as well. It is also possible that evolution in response to novel hosts will influence coevolved relationships

with native hosts as invasive sapinds integrate further into native communities, complicating the local evolutionary dynamics (Carroll and Fox 2008).

It is provocative that the currently evolving phenotypic contrasts between populations on introduced versus native hosts are like those between populations and species exploiting different native hosts. Their global specialization on sapinds, as well as the plants' specialized morphological, chemical, and phenological defenses against them (Carroll and Loye 1987; Aldrich et al. 1990, Carroll et al. 2003), suggest an ancient relationship. Moreover, "Old World" taxa such as *Koelreuteria* were widespread in North America in the Eocene and Paleocene (Arnold 1952; Erwin and Stockey 1990); whether they overlapped then with bug genus *Jadera*, is currently beyond speculation. In recent decades, Taiwanese *K. elegans* has been colonized in the United States by *Jadera* originating from both native *Cardospermum* (southeast) and native *Sapindus* (southwest). The tree also has been colonized in eastern Australia by *Leptocoris* native to *Alectryon*. In each case, the bugs seem to be evolving to match trait values of the tree's Taiwanese seed predator *L. vicinus* (S.P.C. and J.E.L., unpublished data). This scenario of anthropogenic homogenizing adds an improbable but portentous twist to the multidimensional evolutionary chess these insect and plant lineages have probably been playing for millions of years.

Are the plant introductions catalyzing a new and unintended anthropogenic wave of adaptive radiation in these insects? With local adaptation to new hosts occurring in behavior, biochemistry, morphology, phenology, and ecology over just tens of generations (Carroll et al. 2005a; Carroll 2007), it seems possible. At this point, there is no indication of the evolution of pre- or postzygotic reproductive isolation among recently diverged host-associated populations of *J. haematoloma* (S.P.C., unpublished data). Yet, adaptation to new hosts has been accompanied by equally rapid loss of adaptation to native hosts (Carroll et al. 1997, 1998; Carroll 2007). Such performance trade-offs could strongly facilitate continuing host-mediated diversification (*sensu* Strong et al. 1984; Rundle and Nosil 2005; Agrawal et al. 2006; Patten 2008). Investigating additional species and populations of these insects will help to link ongoing diversification with the patterns of host association and coevolution. Data sets that describe preindustrial relationships, for this and other study systems, will help to further illuminate the interplay of history and ongoing microevolutionary processes under contemporary anthropogenic environmental change.

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Appendix. Host records, organized by insect genus and then alphabetically by global region, insect species, and host genus/species within host nativity class (native or introduced)

Genus	Global region	Species	Host	Host nativity	Country	Subfamily	Tribe <sup>a</sup>	Source	
<i>Leptocoris</i>	Africa	<i>aethiops</i> Distant	<i>Allophylus africanus</i> P. Beauv.	Native	Uganda	Sapindoideae	Thoinieae	Field observation	
		<i>annictus</i> Germar	<i>Allophylus africanus</i> (Sond.) De Winter	Native	South Africa	Sapindoideae	Thoinieae	Field observation	
			<i>Allophylus natalensis</i> (Sond.) De Winter	Native	South Africa	Sapindoideae	Thoinieae	Field observation	
		<i>chevreuxi</i> Nouathier	<i>Allophylus pervilletii trifoliatus</i> Radlk.	Native	Zanzibar	Sapindoideae	Thoinieae	Field observation	
		<i>mutillatus</i> Gerstaecker	<i>Cardiospermum grandiflorum</i> Sw.	Introduced	Namibia	Sapindoideae	Paullinieae	Göllner-Scheidig (1997)	
			<i>Cardiospermum corundum</i> L.	Native	Tanzania	Sapindoideae	Paullinieae	Field observation	
			<i>Cardiospermum grandiflorum</i>	Introduced	South Africa	Sapindoideae	Paullinieae	Field observation <sup>b</sup>	
			<i>Cardiospermum haiticacabum</i> L.	Introduced	South Africa	Sapindoideae	Paullinieae	London Museum	
		<i>productus</i> G.-S.	<i>Cardiospermum haiticacabum</i>	Introduced	Uganda	Sapindoideae	Paullinieae	Field observation	
		<i>setdenstaeckeri</i> G.-S.	<i>Paullinia pinnata</i> L.	Native	Ghana	Sapindoideae	Paullinieae	London Museum Natural History	
		<i>tegorovskij</i> G.-S.	<i>Cardiospermum grandiflorum</i> <sup>c</sup>	Native	Uganda	Sapindoideae	Paullinieae	Field observation	
		<i>ursulatae</i> Ferreira et al.	<i>Cardiospermum grandiflorum</i> sp. nov.	Native	Uganda	Sapindoideae	Paullinieae	Field observation	
			<i>abdominalis</i> F.	<i>Schleichera oleosa</i> (Lour.) Oken	Native	India	Sapindoideae	Schleichereae	Malhotra (1958)
			<i>augur</i> F.	<i>Allophylus timorensis</i> (DC.) Blume	Native	Japan	Sapindoideae	Thoinieae	Kohno and Takahashi (2006)
				<i>Schleichera oleosa</i>	Native	India	Sapindoideae	Schleichereae	Malhotra (1958); London Museum Natural History
				<i>Schleichera oleosa</i> <sup>d</sup>	Native	India	Sapindoideae	Schleichereae	National Pusa Collection, India <sup>e</sup>
				<i>Koelreuteria elegans</i>	Native	Taiwan	Sapindoideae	Koelreuterieae	Field observation <sup>f</sup>
		<i>Cardiospermum haiticacabum</i>	Introduced	Taiwan	Sapindoideae	Paullinieae	Field observation		
		<i>Cardiospermum haiticacabum</i>	Introduced	Japan	Sapindoideae	Paullinieae	Kohno and Takahashi (2006)		
		<i>Cardiospermum haiticacabum</i>	Introduced	India	Sapindoideae	Paullinieae	London Museum of Natural History;		
		<i>Cardiospermum haiticacabum</i>	Introduced	Malaysia	Sapindoideae	Paullinieae	National Pusa Collection, India <sup>e</sup> National Institute of Agriculture		
		<i>Cardiospermum haiticacabum</i>	Introduced	China	Sapindoideae	Paullinieae	Japan		
		<i>Allophylus timorensis</i>	Native	Japan	Sapindoideae	Thoinieae	Hoffman (1933)		
		<i>Koelreuteria elegans</i>	Native	Taiwan	Sapindoideae	Koelreuterieae	Kohno and Takahashi (2006)		
		<i>Cardiospermum haiticacabum</i>	Introduced	Japan	Sapindoideae	Paullinieae	Field observation		
		<i>Pometia pinnata</i>	Introduced	Taiwan	Sapindoideae	Paullinieae	Kohno and Takahashi (2006) <sup>g</sup> C.-J. Cheng, personal communication		
		<i>Alectryon oleifolius</i> Reynolds	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)		
		<i>Alectryon subcinereus</i> Radlk.	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)		
		<i>Alectryon tomentosus</i> Radlk.	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)		
		<i>Atalaya hemiglauca</i> F. Muell. ex Benth.	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)		
		<i>Elattostachys xilocarpa</i> (A. Cunn. ex F. Muell.) Radlk.	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)		
		<i>Cardiospermum grandiflorum</i>	Introduced	Australia	Sapindoideae	Paullinieae	Carroll et al. (2005a)		
		<i>Koelreuteria elegans</i>	Introduced	Australia	Sapindoideae	Koelreuterieae	Carroll et al. (2005a)		
		<i>Koelreuteria paniculata</i>	Introduced	Australia	Sapindoideae	Koelreuterieae	Field observation		
	Australia	<i>mitellatus</i> Bergroth	<i>Alectryon oleifolius</i> Reynolds	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)	

## Appendix. Continued

Genus	Global region	Species	Host	Host nativity	Country	Subfamily	Tribe <sup>a</sup>	Source
<i>rufomarginatus</i> F.	Pacific	<i>rufomarginatus</i> F.	<i>Alectryon connatus</i> (F. Muell.) Radlk.	Native	Australia	Sapindoideae	Cupanieae	Field observation
			<i>Alectryon diversifolius</i> Reynolds	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Alectryon tomentosus</i>	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Allophylus cobbe</i> (L.) Raeusch.	Native	Australia	Sapindoideae	Thouinieae	Carroll et al. (2005a)
			<i>Elattostachys xylocarpa</i>	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Jagera pseudorhus</i> (A. Rich.) Radlk.	Native	Australia	Sapindoideae	Cupanieae	R. Whyte, personal communication <sup>b</sup>
			<i>Alectryon connatus</i>	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Alectryon coriaceus</i> (Benth.) Radlk.	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Alectryon diversifolius</i>	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Alectryon oleifolius</i>	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Alectryon subcinereris</i>	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Alectryon subdentatus</i> (Radlk.)	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Alectryon tomentosus</i>	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Allophylus cobbe</i>	Native	Australia	Sapindoideae	Thouinieae	Carroll et al. (2005a)
			<i>Atalaya hemiglauca</i>	Native	Australia	Sapindoideae	Sapindoideae	Carroll et al. (2005a)
<i>Atalaya salicifolia</i> (DC.) Blume	Native	Australia	Sapindoideae	Sapindoideae	Carroll et al. (2005a)			
<i>Jadera</i>	North America	<i>Jadera</i>	<i>Elattostachys xylocarpa</i>	Native	Australia	Sapindoideae	Cupanieae	Carroll et al. (2005a)
			<i>Jagera pseudorhus</i>	Native	Australia	Sapindoideae	Cupanieae	R. Whyte, personal communication
			<i>Cardiospermum grandiflorum</i>	Introduced	Australia	Sapindoideae	Paullinieae	Carroll et al. (2005a)
			<i>Koelreuteria elegans</i>	Introduced	Australia	Sapindoideae	Koelreuteriaceae	Carroll et al. (2005a)
			<i>Schleichera oleosa</i>	Introduced	Australia	Sapindoideae	Schleichereae	Carroll et al. (2005a)
			<i>Pometia pinnata</i> J.R. Forst. & G. Forst.	Introduced	French Polynesia	Sapindoideae	Nephelieae	USNM
			<i>Allophylus [ternatus]</i> Lour. <sup>c</sup>	Native	Caroline Isl. Lele	Sapindoideae	Thouinieae	USNM
			<i>Allophylus cobbe</i>	Native	New Guinea	Sapindoideae	Thouinieae	Braekman et al. (1982)
			<i>Allophylus [ternatus]</i>	Native	Marshall Islands	Sapindoideae	Thouinieae	Gross (1960)
			<i>Allophylus [ternatus]</i>	Native	Marshall Islands	Sapindoideae	Thouinieae	USNM
			<i>Allophylus [ternatus]</i>	Native	Caroline Isl. Palau	Sapindoideae	Thouinieae	Gross (1960)
			<i>Cardiospermum corindum</i>	Native	USA-Florida	Sapindoideae	Paullinieae	Field observation
			<i>Serjania brachycarpa</i> A. Gray ex Radlk.	Native	USA-Texas	Sapindoideae	Paullinieae	Field observation
			<i>Urvillea ulmacea</i> Kunth	Native	USA-Texas	Sapindoideae	Paullinieae	Field observation
			<i>Cardiospermum halicacabum</i>	Introduced	USA-Texas	Sapindoideae	Paullinieae	Field observation
<i>Paullinia sessiflora</i> Radlk.	Native	Mexico-Jalisco	Sapindoideae	Paullinieae	Field observation			
<i>Cardiospermum corindum</i>	Native	USA-Florida; Mexico-Baja California, Puebla	Sapindoideae	Paullinieae	Carroll and Loye (1987); field observation			
<i>Sapindus oahuensis</i> Hillebr. ex Radlk.	Native	USA-Hawaii	Sapindoideae	Sapindeae	Carroll and Loye (1987)			
<i>Sapindus saponaria drummondii</i> (Hook. & Arn.) L.D. Benson	Native	USA	Sapindoideae	Sapindeae	Carroll and Loye (1987)			

Appendix. Continued

Genus	Global region	Species	Host	Host nativity	Country	Subfamily	Tribe <sup>a</sup>	Source
			<i>Sapindus saponaria saponaria</i> L.	Native	USA-Hawaii	Sapindoideae	Sapindae	Field observation
			<i>Serjania brachycarpa</i>	Native	USA	Sapindoideae	Paullinieae	Carroll and Loye (1987)
			<i>Cardiospermum halitacabum</i>	Both	USA	Sapindoideae	Paullinieae	Porter (1917), Carroll and Loye (1987)
			<i>Cardiospermum grandiflorum</i>	Introduced	USA-California and Hawaii	Sapindoideae	Paullinieae	Field observation
			<i>Cardiospermum halitacabum</i>	Introduced	Bahamas	Sapindoideae	Paullinieae	Field observation
			<i>Koelreuteria bipinnata</i> Franch.	Introduced	USA	Sapindoideae	Koelreuterieae	Field observation
			<i>Koelreuteria elegans</i> (Seem.) A. C. Smith	Introduced	USA	Sapindoideae	Koelreuterieae	Carroll and Loye (1987)
			<i>Koelreuteria paniculata</i> Laxm.	Introduced	USA	Sapindoideae	Koelreuterieae	Carroll and Loye (1987)
			<i>Sapindus mukorossi</i> Gaertn.	Native	USA	Sapindoideae	Sapindae	Field observation
			<i>Cardiospermum corindum</i>	Introduced	USA-Florida	Sapindoideae	Paullinieae	Field observation
			<i>Koelreuteria elegans</i>	Introduced	USA-Florida	Sapindoideae	Koelreuterieae	Field observation
			<i>Paullinia turbacensis</i> Kunth.	Native	Panama	Sapindoideae	Paullinieae	Carroll and Loye (1987)
			<i>Serjania mexicana</i> (L.) Willd.	Native	Panama	Sapindoideae	Paullinieae	Carroll and Loye (1987)
			<i>Thinouia migrantha</i> Triana & Planch.	Native	Panama	Sapindoideae	Paullinieae	Carroll and Loye (1987)
						<i>Cardiospermum grandiflorum</i>	Native	Costa Rica
<i>Paullinia turbacensis</i>	Native	Panama				Sapindoideae	Paullinieae	Carroll and Loye (1987)
<i>Serjania mexicana</i>	Native	Panama				Sapindoideae	Paullinieae	Carroll and Loye (1987)
<i>Thinouia migrantha</i>	Native	Panama				Sapindoideae	Paullinieae	Carroll and Loye (1987)
<i>Cardiospermum grandiflorum</i>	Native	Belize				Sapindoideae	Paullinieae	Field observation
<i>Serjania</i> sp.	Native	Colombia				Sapindoideae	Paullinieae	Field observation
<i>Cardiospermum halitacabum</i>	Native	Brazil				Sapindoideae	Paullinieae	Panizzi and Hirose (2002)
<i>Allophylus edulis</i> (A.St.-Hil., A. Juss. & Combess.) Hieron. Ex Niederl.	Native	Brazil				Sapindoideae	Paullinieae	Thum and Costa (1997)
<i>Sanguinolenta silbergliedi</i> Froeshner	Native	Ecuador-Galapagos				Sapindoideae	Paullinieae	Froeshner (1985)
<i>Cardiospermum</i> sp.	Native	South Africa				Sapindoideae	Macphersonieae	South African National Collection of Insects <sup>20</sup>
<i>Pappea capensis</i> Eckl. & Zeyh.	Introduced	South Africa				Hippocastanoideae	Aceraceae	South African National Collection of Insects
<i>Acer buergerianum</i> Miq.	Native	India				Sapindoideae	Sapindae	London Museum
<i>Sapindus trifoliatus</i> L.	Native	India				Sapindoideae	Sapindae	Kaur et al. (1984)
<i>Sapindus mukorossi</i>	Native	USA				Hippocastanoideae	Aceraceae	Carroll and Loye (1987)
<i>Acer negundo</i> L.	Native	USA				Hippocastanoideae	Aceraceae	Carroll and Loye (1987)
<i>Acer saccharinum</i> L.	Introduced	USA	Hippocastanoideae	Aceraceae	Field observation			
<i>Koelreuteria bipinnata</i>	Introduced	USA	Sapindoideae	Koelreuterieae	Field observation <sup>6</sup>			
<i>Koelreuteria paniculata</i>	Introduced	USA	Sapindoideae	Koelreuterieae	Field observation <sup>7</sup>			
<i>Boisea</i>	Africa	<i>obscura</i> Westwood						
		<i>sanguinolenta</i> silbergliedi Froeshner						
		<i>fulcrata</i> Germar						
	Asia	<i>coimbatorensis</i> Gross						
		<i>rubrolineata</i> Barber						

Appendix. Continued

Genus	Global region	Species	Host	Host nativity	Country	Subfamily	Tribe <sup>a</sup>	Source
		<i>tritittata</i> Say	<i>Acer negundo</i> <i>Sapindus saponaria drummondii</i>	Native Native	USA USA-Southwestern	Hippocastanoideae Sapindoideae	Acerae Sapindeae	Field observation Field observation
			<i>Acer grandidentatum</i> Nutt. <i>Acer saccharinum</i> <i>Acer buergerianum</i> <i>Acer ginnala</i> Maxim.	Introduced Introduced Introduced Introduced	USA-Texas USA-Oklahoma USA-South Carolina USA-Minnesota	Hippocastanoideae Hippocastanoideae Hippocastanoideae Hippocastanoideae	Acerae Acerae Acerae Acerae	Reinert et al. (1999) Field observation Field observation <sup>o</sup> Field observation

Field observations are by the authors except as noted.

<sup>a</sup> Tribal designations are based on applying conventional nomenclature to the tribe-level groups proposed by Buerki et al. (2009).

<sup>b</sup> Personal communication with photodocumentation from D. Simelane, Agricultural Research Council, South Africa.

<sup>c</sup> Based on strong readily evident morphological differences, we judge *C. grandiflorum* native in eastern Africa to be a different species from the ostensibly conspecific Neotropical variety that is an invasive alien in southern Africa (and elsewhere).

<sup>d</sup> Specific epithet updated from the labeled "*Scheitchera trijuga*."

<sup>e</sup> Inspected and communicated by Paula Mitchell (Winthrop University).

<sup>f</sup> Personal communication with photodocumentation from K. Barker (Pingtung, Taiwan).

<sup>g</sup> These authors give host records for *L. rufomarginatus* and what they identify as *L. augur*. Inspection of photographs provided for our inspection by the lead author (K. Kohno, personal communication), which include male genitalia, show that the specimens they identified as *L. augur* from *C. halicacabum* (and by inference probably also those from *A. timorensis*) are instead *L. vicinus*. Pinned *L. vicinus* from the collection of the National Institute of Agriculture Japan, tagged with "*Cardiospermum*" are probably likewise from *C. halicacabum*.

<sup>h</sup> Video of captive *L. rufomarginatus* feeding on seed of *J. pseudorhus* (on which bugs were maturing in nature) at [http://www.saveourwaterwaysnow.com.au/01\\_cms/details\\_pop.asp?ID=933#2315](http://www.saveourwaterwaysnow.com.au/01_cms/details_pop.asp?ID=933#2315).

<sup>i</sup> Corrected from typed labels reading "*Ponachia pinnata*" on the judgement that the nonexistent genus was mistranscribed from a handwritten label reading "*Ponettia pinnata*."

<sup>j</sup> *Allophylus* species based on Republic of the Marshall Islands Biodiversity Clearing House Mechanism ([http://biormi.org/index.shtml?en/native\\_plants.shtml](http://biormi.org/index.shtml?en/native_plants.shtml)).

<sup>k</sup> This taxon is *J. aeola* of Gölner-Scheidt (1979); here, we follow Henry (1988).

<sup>l</sup> Based on Gölner-Scheidt's original circumscription of *J. sangainolepta* to the Caribbean, Barcellos et al. (2008) suggested that this Brazilian record might be the superficially similar *J. aeola*. However, the museum holdings from which Gölner-Scheidt generalized are probably insufficient in scope to judge with certainty based on range alone.

<sup>m</sup> Also, personal communication with photodocumentation of juveniles and adults in Namibia, from Jürgen Deckert (Naturkunde Museum, Berlin).

<sup>n</sup> Made by S.P.C. and P. Jorgensen.

<sup>o</sup> Personal communication with photodocumentation from G. and C. Bruce, South Carolina.