

Specialization of *Jadera* Species (Hemiptera: Rhopalidae) on the Seeds of Sapindaceae (Sapindales), and Coevolutionary Responses of Defense and Attack

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ABSTRACT Feeding and breeding associations of five species of *Jadera* on 11 species of sapindaceous plants in the United States and Panama are described. Ecological notes are given for each species on its particular host plants. Nonsapindaceous plants used during reproductive diapause are also listed. The consistency with which *Jadera* use seeds of these plants for reproduction suggests that they are specialists on this plant family. This idea is supported by concordance in distributions of the insects and their host plants, presence in the plants of morphological and phenological characters that directly reduce impact of seed predators, and evidence of coevolution between mouthpart morphology and seed defense structures. This paper provides strong evidence that serinethine rhopalids evolved on host plants in the Sapindales.

KEY WORDS coevolution, Hemiptera, *Jadera*, phenology

An Ode to Sapindaceae

What wondrous beauty, strength and grace
Your forms have painted on earth's face!
In forest dark, and damp and hot
Nephelium rises on the spot
Where fowl alight, in weary flight,
And view thereon a glorious sight
of luscious fruits, so red, so rare
That birds and beasts compete to share.
And far beyond, in cooler climes,
Sapindus berries cleanse the line
Of clothes, which man since Adam wears;
And oft' alas! in labor tares.
But stranger still, on China's soil,
Where men of will so bravely toil,
Is *Litchi*, loved, and culture trained;
And *Koelreuteria*, 'Golden Blossoms' rained.
—G. Weidman

TRUE BUGS of the genus *Jadera* Stål consist of about 18 species distributed in tropical and subtropical America (Göllner-Scheiding 1979, 1982). One species, *Jadera haematoloma* (Herrich-Schaeffer), ranges as far north as the central United States, and another, *Jadera aeola* (Dallas), ranges southward into Argentina. These insects are fairly common in museum collections, and in the field form prominent aggregations. Systematic treatments are given by Schaefer (1965, 1978), Chopra (1967), Schaefer & Chopra (1982), and Göllner-Scheiding (1979, 1982, 1983).

What is known of the biology of *Jadera* in the wild comes from host-plant records made by Davis

(1969) and Gagné (1971), after *Jadera haematoloma* was introduced to Hawaii, where they observed it on trees and vines of the family Sapindaceae (order Sapindales). Noting that members of the related genus *Leptocoris* Hahn also feed on Sapindales, Schaefer & Mitchell (1983) suggested that the serinethine rhopalids (consisting of these two genera only) are specialists on that plant group. Extensive host-plant records, however, have not been available for *Jadera*. Here we report the feeding associations of five species of *Jadera* on the seeds of 11 species of plants in the family Sapindaceae. Evidence is presented that these bugs do specialize on Sapindaceae.

Materials and Methods

Results are based on field observations of bugs and plants in the southern United States (1980-85) and on Barro Colorado Island in central Panama (March and April 1985), and notes taken from specimens in the National Museum of Natural History (NMNH) and the American Museum of Natural History (AMNH).

Field work in the United States was conducted on bugs in August 1982 and October 1984 (Cochise and Santa Rita Counties, Ariz.); August 1982 (Mora County, N. Mex.); from September 1980 to September 1983 and September 1984 (Caddo, Cleveland, Cotton, Oklahoma, and Woodward Counties, Okla.); and August 1984 and January, May, and December 1985 (Dade, Lee, Monroe, and Polk Counties, Fla.). Plants were examined for the presence of *Jadera* and, when bugs were located, their feeding behavior and reproductive condition were recorded. "Host plant" refers to those species upon which *Jadera* has been observed to feed for reproduction. Observations of mating adults, or of

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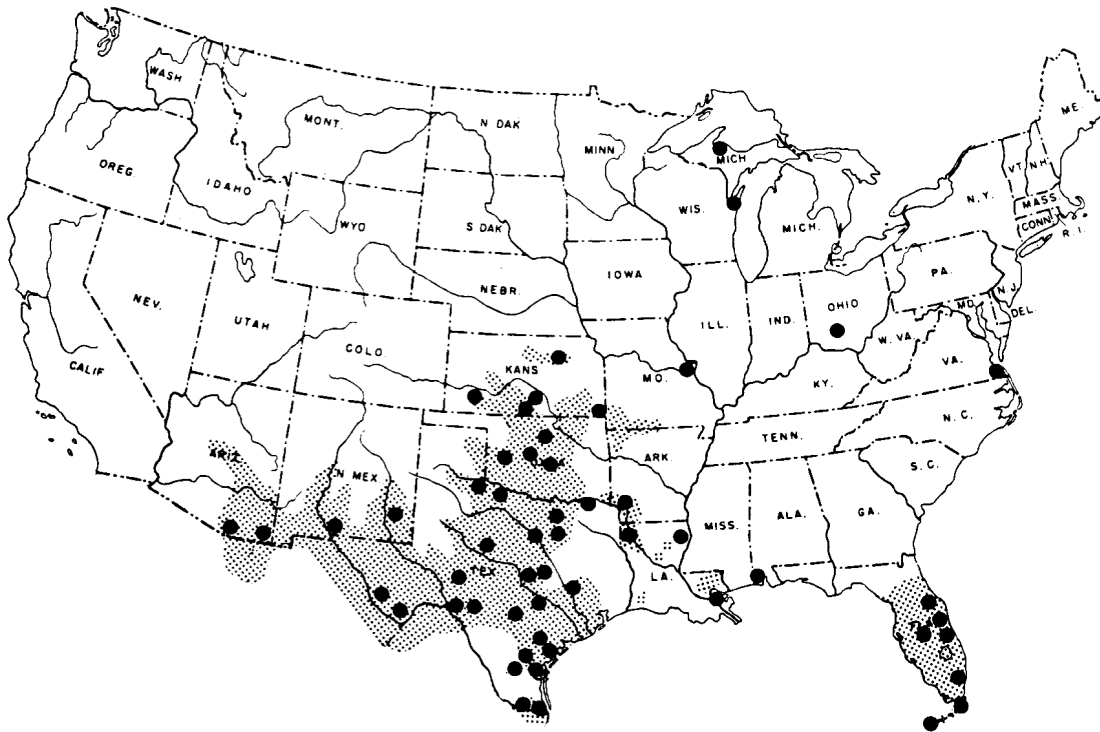


Fig. 1. Concordance between the distributions of *J. haematoloma* (●) and its native sapindaceous host plants (stippled, *S. saponaria* var. *drummondii* in the southwest and south central states, *C. corindum* in Florida).

nymphs and adults feeding on the seeds of a plant, were considered as evidence that the plant was serving as a host. In Panama, the host plants were large vines that grow into the forest canopy, and observations on these were limited to fallen seeds on the forest floor.

Observations of host-plant phenology were made throughout the study period. Additional phenological data were taken from the herbaria of the University of Florida, Gainesville, and the Fairchild Tropical Gardens, Miami, Fla., and from Croat (1978).

The number of bugs in aggregations was either counted directly for groups of less than a few hundred or estimated by counting the number of bugs in an area 1 m² and multiplying by the number of areas in the main body of the aggregation. This latter technique was useful because the bugs were rather uniformly distributed in most aggregations. Estimates for aggregations of $\geq 1,000$ are coarse. The incidence of bugs was determined by comparing the numbers of seed-bearing host plants at which bugs were present with the total number of such plants examined. At some individual plants, bugs were observed to disappear seasonally (e.g., in winter), but to recolonize the plants later (e.g., in summer). Such recolonizations are treated as separate samples in the data on incidence.

The museum collections were used to chart the bugs' distributions and for host records. Host-plant distributions were taken from Brizicky (1964), Little (1976), and Croat (1976, 1978).

Body lengths and beak lengths of *Jadera haematoloma* were measured for alcoholic specimens collected on *Sapindus* in Oklahoma ($n = 20$) and on *Cardiospermum* in Florida ($n = 20$), using dial calipers with 0.02-mm gradation. Body lengths were measured as the distance from the anterior tip of the clypeus to the tips of the closed elytra, which extended posteriorly beyond the abdomen. Beak lengths were measured from the tip of the clypeus to the distal tip of the beak. The same dial calipers were used for measuring the dimensions of 20 fruiting capsules of two individuals of *Cardiospermum corindum* (L.). Measurements were compared with the nonparametric Mann-Whitney *U* test.

Results and Discussion

Host Plants. *Jadera* has been found reproducing only on the seeds of sapindaceous plants, and occurs more often than not on seed-bearing hosts (Table 1). *Sapindus saponaria* L. var. *drummondii* (Hook. & Arn) Benson, the soapberry tree, is the main host plant of *J. haematoloma* in the southwestern and south central United States (Fig. 1). In Oklahoma, this tree flowers in late spring and matures seed in late summer. Large aggregations of the bug form by late summer each year, feeding on the developed embryos. The introduced golden rain tree, *Koelreuteria paniculata* (Laxm.), is also commonly used as a host plant in the southern United States. In southern Texas, large

Table 1. Host plants of *Jadera* species

<i>Jadera</i> species and host plant	Locality	No. bugs ^a	Incidence ^b	Source
<i>J. haematoloma</i>				
<i>S. saponaria</i> var. <i>drummondii</i>	Arizona ^c	10-100	3/3	S.P.C. & J.E.L. ^d
	Kansas	—	—	NMNH
	Oklahoma ^c	0-10,000	8/11	S.P.C. & J.E.L. ^d
var. <i>oahuensis</i> (Hillebr.)	Hawaii ^c	"Abundant"	—	Gagné (1971)
<i>K. paniculata</i> ^e	Florida ^c	50-2,000	2/2	S.P.C. & J.E.L. ^d
	Georgia	—	—	NMNH
	Missouri	—	—	NMNH
	New Mexico ^c	15	1/1	S.P.C. & J.E.L. ^d
	Oklahoma ^c	10-2,500	29/30	S.P.C. & J.E.L. ^d
<i>K. elegans</i> ^e	Florida	10-5,000	2/2	S.P.C. & J.E.L. ^d
	Hawaii ^c	"Large numbers"	—	Gagné (1971)
<i>Cardiospermum halicacabum</i> (L.) ^e	Mississippi ^c	—	—	W. Jones ^f
	Hawaii ^c	"Heavy"	—	Davis (1969)
<i>C. corindum</i>	Florida ^c	0-1,000	12/26	S.P.C. & J.E.L. ^d
<i>S. brachycarpa</i>	Texas	"Numerous"	—	F. & P. Mitchell ^f
<i>J. sanguinolenta</i>				
<i>K. elegans</i> ^e	Florida ^c	10,000	1/2	S.P.C. & J.E.L. ^d
<i>Litchi chinensis</i> ^e	Florida	—	—	F. Mead ^f
<i>J. antica</i>				
<i>C. corindum</i>	Florida ^c	0-5	2/26	S.P.C. & J.E.L. ^d
<i>K. elegans</i> ^e	Florida	0-1	1/2	S.P.C. & J.E.L. ^d
<i>J. aeola</i>				
<i>Serjania decaplueria</i> (Croat)	Panama ^c	50-1,000	3/3	S.P.C. & J.E.L. ^d
<i>Serjania mexicana</i> (L.)	Panama ^c	50-1,000	5/5	S.P.C. & J.E.L. ^d
<i>T. myriantha</i>	Panama ^c	0-1,000	10/19	S.P.C. & J.E.L. ^d
<i>Paullinea turbacensis</i> (H.B.K.)	Panama ^c	0-3,000	4/12	S.P.C. & J.E.L. ^d
<i>J. obscura</i>				
<i>S. decaplueria</i>	Panama ^c	50-1,000	3/3	S.P.C. & J.E.L. ^d
<i>S. mexicana</i>	Panama ^c	0-1,000	3/5	S.P.C. & J.E.L. ^d
<i>T. myriantha</i>	Panama ^c	50-15,000	19/19	S.P.C. & J.E.L. ^d
<i>P. turbacensis</i>	Panama ^c	0-3,000	6/12	S.P.C. & J.E.L. ^d

^a Adults or nymphs, or both, on one plant or a cluster of plants.

^b Number of plants infested per number of plants examined.

^c Adults and nymphs present; feeding.

^d Personal observation.

^e Introduced to the United States.

^f Personal communication.

numbers of adult and juvenile *J. haematoloma* have also been observed on the vine *Serjania brachycarpa* (Gray) (F. & P. Mitchell, personal communication).

Coincident with the United States distribution of its other native host, *J. haematoloma* also occurs in southern Florida on the balloon vine or heartseed, *C. corindum* (Fig. 1). The bug also uses two species of *Koelreuteria* in central and southern Florida. *S. saponaria* L., a tropical soapberry that occurs as a disjunct in Florida, was not colonized by *Jadera* at any of five sites in the upper Florida Keys. This was true in May and December samples, when *J. haematoloma* was common on nearby fruiting *C. corindum*, and also in January and August when *J. haematoloma* was less common on *C. corindum*, which was producing fewer seeds at these times. The enlarged and hardened drupe of *S. saponaria* may prevent bugs from gaining access to the seeds. Manually opened seeds of this variety were readily fed on by captive *J. haematoloma* in Florida ($n = 20$ adults on five seeds).

Jadera sanguinolenta (F.) and *Jadera antica* (Walker) are primarily tropical species that range

northward into southern Florida. *J. sanguinolenta* breeds in large numbers on specimens of *Koelreuteria elegans* (Seem.) Sm. in the Fairchild Tropical Gardens in Miami. This bug has also been recorded on cultivated *Litchi chinensis* (Sonn.) in south Florida (F. Mead, personal communication). *J. antica* occurs in small numbers in south Florida; we have observed a total of six individuals: three single males, plus one mating pair, on *C. corindum*, and one male on *K. elegans*. Twelve nymphs from eggs laid by the female *J. antica* were raised to adulthood on seeds of *C. corindum*. After their terminal molt, these 12 continued to feed on seeds of *C. corindum*, but they did not become reproductively active, and all were dead within 40 d of the final molt.

Jadera aeola and *Jadera obscura* (Westwood) were observed on four species of vining host plants in Panama. These hosts set seed mainly during the January-April dry season (Croat 1978), and it appears that the reproductive activities of the bugs are concentrated in that period (H. Wolda, personal communication). *J. obscura* is most abundant on *Thinouia myriantha* (Tr. & Planch.), and

many thousands of nymphs were often found feeding on the fallen samaras of a single vine. Captive adult *J. aeola* and *J. obscura* raised from nymphs fed and reproduced on the seeds of these four host plants, but reproductive adults in the wild were only observed feeding on the seeds of these four plants on two occasions. They may feed on the seeds high in the forest canopy before they fall.

Other Plant Associations. Adult *Jadera* were rarely observed away from sapindaceous host plants, and the flightless nymphs, never. The United States distribution of *J. haematoloma* in the museum collections corresponds almost exactly to that of its two native host plants (Fig. 1), as would be expected if it is a specialist on these species.

Diapausing *J. haematoloma* does not feed during the cold winter months in Oklahoma (Carroll 1983), but in Florida, where diapause occurs during warm weather, we have observed this species to take nectar from flowering *Bidens* sp. (Asteraceae), as well as fluid from the petioles of the introduced host tree *K. elegans*. Large diapausing aggregations of *J. obscura* in Panama suck fluids from the petioles and major leaf veins of a variety of nonsapindaceous understory trees, sometimes killing the leaves.

Other nonsapindaceous plants are listed with the specimens of *J. haematoloma* in the NMNH and the AMNH: *Clematis*, *Mimosa*, *Albizia*, *Typhalatifolia*, cotton, wheat, and corn. None of these records specifically notes feeding, but any of these species could serve as resting sites or stem and flower feeding sites for nonreproductive adults. No nonsapindaceous hosts are noted for any of the nymphs (i.e., nonvolant individuals) in these collections.

Cannibalism and Entomophagy. *J. haematoloma* in the field was observed to feed opportunistically on teneral conspecifics and on a variety of disabled or freshly dead arthropods. Most entomophagy was by nymphs or reproductive females (15 observations of females, 9 of nymphs, and 4 of males). Teneral individuals are often fed on and killed in captive groups.

Sapindaceae/*Jadera* Coevolution. Several of the host plants show characters that appear to act specifically or in part to deter seed predation by *Jadera*. The single spherical seed of *Sapindus saponaria* var. *drummondii* is covered by a moist, fleshy drupe that functions not only to attract avian seed dispersers, but also prevents young nymphs from gaining access to the seeds. The combined thickness of the drupe and the seed coat is great enough to prevent access to the embryo by instars I-III, limiting them to feeding on fallen seeds in which the drupe is damaged. The long proboscis of *J. haematoloma*, which extends more than half the length of the body, allows advanced nymphs and adults access to the drupe-covered seeds. However, these bugs most frequently feed with the younger

instars on fallen fruits in which the seeds are exposed. Many fruits are held on the branches through the winter and attract flocks of cedar waxwings (Aves: *Bombycilla cedrorum* Vieillot), which disperse the seeds. The ovoid fruits of this *Sapindus* subspecies are ca. 1.5 by 1.3 cm, the size of crab apples, as large a fruit as is apparently ingestible by this bird (Bent 1950). The need for seed dispersal by this agent may, thus, put an upper limit on the dimensions of the protective drupe that are reproductively advantageous.

The fruiting phenology of *S. saponaria* var. *drummondii* may also serve to reduce seed predation. In Oklahoma, this plant may flower any time between late May and early July, much later than most other American trees at this latitude, and it does not mature its seeds until late August and September. Because *J. haematoloma* in this region enters reproductive diapause and ceases feeding in early October (Carroll 1983), late seeding by the host plant minimizes the period during which bug populations may build and seed predation may take place.

In contrast, *S. saponaria* in Florida cannot escape from *J. haematoloma* phenologically because the bug does not enter a seasonal diapause in this climate (S.P.C., unpublished data). Instead of serving to attract fruit-eating animals, the drupe dries into a dense leathery shell that is unattached to the seed within. The fruit is about 50% larger in diameter than that of *S. saponaria* var. *drummondii*, and may be produced at any time of year. The seeds are apparently dispersed mainly by ocean currents (Guppy 1917), and the plant is limited to the "transition zone" between the mangroves and the hardwood hammocks in the upper Florida Keys. Whether year-round seed predation forced the subtropical *S. saponaria* away from a soft drupe suitable for animal dispersal, or modifications for water-borne dispersal took place independently of seed predation, is not certain.

Cardiospermum, the aptly named balloon vine, has the intriguing feature of inflating its capsules with gas into taut spheres, ca. 3 cm in diameter in *C. corindum*. Three vertical septa at 120° angles form internal supports that suspend three seeds at the balloon's center (Fig. 2). This organization maximizes the distance between the seeds and the balloon wall and, thus, also the distance between the seeds and the bugs, which cut tiny holes in the wall to gain entrance into the seed chamber. Only the single seed in a particular chamber can be reached from one entrance hole. When the seeds are mature, the balloon wall dries and the capsule splits into three parts, each with a seed and a septum to carry it on the wind.

J. haematoloma in Florida circumvent this defense in at least four ways. First, they attain a larger body size than in Oklahoma ($\bar{x} \pm SD = 13.95 \pm 0.81$ versus 12.40 ± 0.68 mm, respectively; $U = 21$; $P < 0.001$; Mann-Whitney U test), and have mouthparts (beaks) that are longer in

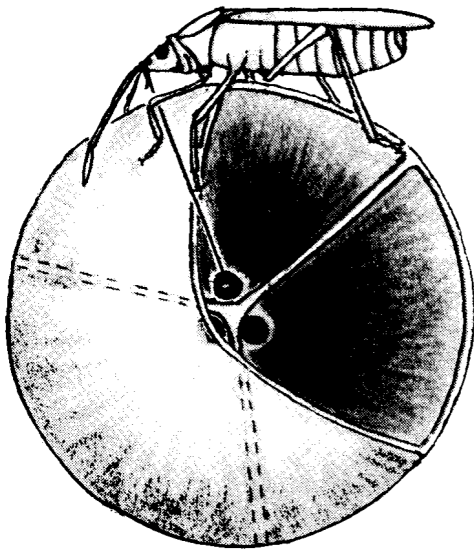


Fig. 2. Adult female *J. haematoloma* feeding on a seed of the balloon vine, *C. corindum* (somewhat stylized). Depicted is the internal structure of the capsule, which holds the three seeds internally at a distance of ca. 1 cm from the protective outer wall. Populations of this *Jadera* species that have specialized on this host plant have longer mouthparts than those that feed on *Sapindus*, which does not defend its seeds in this way (see text and Fig. 3).

absolute size (9.78 ± 0.79 versus 7.12 ± 0.42 mm, respectively; $U = 0$; $P < 0.001$) and also longer in relation to body length (70 ± 4 versus $57 \pm 3\%$, respectively; $U = 0$; $P < 0.001$) (Fig. 3). Thus, a typical Florida bug will be able to reach farther with its proboscis, and, for a given body size, has a reach ca. 12% greater than that of an Oklahoma bug. The average minimal distance between the walls of the mature capsules and seeds of *C. corindum* was 10.9 ± 0.5 mm (range, 9.6–11.7 mm), somewhat greater than the average length of the mouthparts of adult female *J. haematoloma* collected in this habitat. However, the range of mouthpart lengths was from 8.6 to 10.8 mm, so many adults are probably able to reach the seeds at the center of fully inflated capsules. Second, reproductive females sometimes feed on the immature seeds in partially inflated young balloons. Third, bugs gain entrance to mature capsules that are beginning to split open just prior to wind dispersal, or feed on fallen seeds that have not dispersed far from the plant. Fourth, females sometimes oviposit in small openings in the capsule wall, their offspring developing on the seeds within the capsule.

The tropical vines in Panama have fewer morphological defenses against *J. aeola* and *J. obscura*. From the massive aggregations of juveniles on the fallen seeds of *Thinouia* and *Serjania*, it is clear that dispersing away from the parent plant reduces the predation rate, and these plants attempt to accomplish this with wind-dispersed sa-

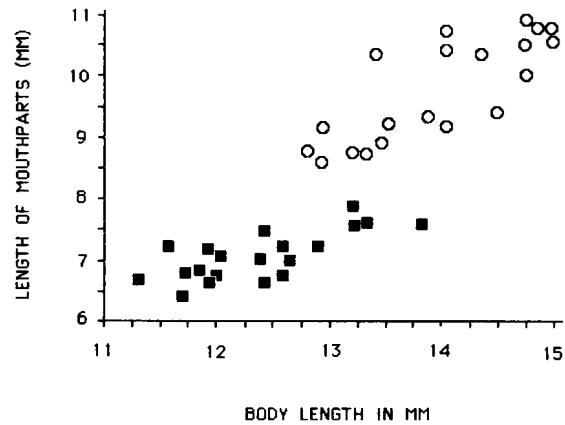


Fig. 3. Comparative length of the mouthparts in relation to the length of the body for adult female *J. haematoloma* in Florida (O) and Oklahoma (■).

maras. *Paullinea* seeds are dispersed by birds and mammals (Croat 1976). The synchronized annual seed production by these host plants may act to swamp the predator population to some extent. Synchrony was especially strong within the *Thinouia* on Barro Colorado Island, so the semispecialist *J. obscura* may be limited to one generation per year. During the wet season, when host seeds are not available, this bug forms persistent aggregations of up to several hundred thousand diapausing adults (personal observation; H. Wolda, personal communication).

General Discussion

Evidence is presented that the five *Jadera* species studied thus far reproduce exclusively on the seeds of plants of the family Sapindaceae. This evidence includes the absence of observations of the bugs reproducing on other plant species, the concordance of the geographical distributions of the bugs and the host plants, the regularity with which the bugs may be found on seed-bearing host plants, the evolution of specific defenses by the host plants, and traits that function to overcome these defenses in the bugs.

The four genera of vining host plants, *Cardiospermum*, *Paullinea*, *Serjania*, and *Thinouia*, are all members of the sapindaceous tribe Paullinieae (Brizicky 1964, Croat 1976). Thus, the occurrence of *J. haematoloma*, *J. obscura*, *J. aeola*, and *J. antica* on this group suggests some conservatism in the range of host plants utilized. However, *J. haematoloma* also feeds on *Sapindus* in the Sapindaceae and has adopted the introduced *Koelreuteria*, as has *J. sanguinolenta*. (The report by Aldrich et al. [1979] of *J. haematoloma* on *Ficus* in Florida cannot be confirmed as a feeding record [J. Aldrich, personal communication].) The comparatively very short labium of *J. antica* (ca. 4 mm in length) suggests that the species probably often feeds on hosts other than *Cardiospermum*,

but these are at present unknown. The closely related *Urvillea* should also be examined as a possible host for *Jadera*. In southern Texas it could be a host of either *J. haematoloma* or *J. hinnulea* Bayard.

Leptocoris, the closest relative of *Jadera*, is also a specialist on Sapindales. In North America it feeds on Aceraceae (Schaefer 1975), in India on Sapindaceae (Malhotra 1958), in China on Sapindaceae (Hoffman 1933), in Australia on Sapindaceae and Rutaceae (Kumar 1966), and in Micronesia on Sapindaceae (Gross 1963). Evidence for the specialization of *Jadera* on sapindaceous hosts, presented here, further indicates an ancient association and radiation of the rhopalid subfamily Serinethinae on the Sapindales.

We observed five individuals of *J. saguinolenta* on *C. corindum* in Monroe County, Fla., in January 1987.

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