

**ECOLOGY OF *AMBLYCERUS CRASSIPUNCTATUS* RIBEIRO-COSTA
(COLEOPTERA: BRUCHIDAE) IN SEEDS OF HUMIRIACEAE, A NEW HOST
FAMILY FOR BRUCHIDS, WITH AN ECOLOGICAL COMPARISON TO
OTHER SPECIES OF *AMBLYCERUS***

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Abstract

In Venezuela *Amblycerus crassipunctatus* Ribeiro-Costa feeds in seeds of *Vantanea minor* Bentham, Humiriaceae, a new host family for the Bruchidae. Species of *Amblycerus* Thunberg now are known to feed in from 11 to 14 families of plants, more than any other bruchid genus. Ecological relationships of *A. crassipunctatus* with its host were compared to *A. nigromarginatus* (Motschulsky), *A. luteonotatus* (Pic), *A. dispar* (Sharp), *A. guazumicola* Kingsolver and Johnson, *A. vitis* (Schaeffer), *A. acapulcensis* Kingsolver, *A. robiniae* (Fabricius), *A. hoffmanseggii* (Gyllenhal), *A. testaceus* (Pic), *A. submaculatus* (Pic), *A. cistelinus* (Gyllenhal), *A. longesuturalis* (Pic), and *A. schwarzi* Kingsolver and their hosts. *A. crassipunctatus* damaged 28.5% to 39% of *V. minor* fruits examined. In other species of *Amblycerus* where these figures are available, from 01.0% to 61% of the fruits were damaged. We found that eggs of almost all of the species discussed have a similar flange with glue on the periphery. This kind of attachment may prevent the egg from becoming detached from the fruit as it matures and during eclosion of the first instar larva or protect eggs against mechanical injuries. Larvae of most species of *Amblycerus* feed in several seeds during their development, but *A. dispar* and *A. vitis* feed in only one seed. Apparently almost all species of *Amblycerus* spin a cocoon for pupation. This was evolved probably because the large size of the adults led to the habit of feeding in several seeds. Most bruchids are much smaller in body size than species of *Amblycerus* and thus pupate inside a single seed that negates the need for a cocoon.

More than 100 species of *Amblycerus* Thunberg have been described in the New World, but we estimate that more than 100 more will eventually be found and described, especially in Central and South America. Species of *Amblycerus* feed in seeds of forest trees and shrubs and of ornamental plants. None of the host plants are considered to be major agricultural crops, but when their seeds are destroyed by bruchids, the potential for regeneration of plants in forestry

plantings and those used for fuel, honey and ornamental plantings is reduced. Biological and ecological data, however, are scarce for this genus.

Most of the research on the genus *Amblycerus* until about 1970 was limited to taxonomy. Kingsolver (1970, 1975, 1976, 1980, 1991) pioneered the modern-day interest in the systematics of *Amblycerus*. Recently Kingsolver *et al.* (1993), Genaro and Kingsolver (1997) and Kingsolver and Ribeiro-Costa (1997) published new species descriptions, etc. Significant revisionary studies were completed recently by Ribeiro-Costa (1995) for Brazil and Romero *et al.* (1996) for the United States and Mexico. Ribeiro-Costa has published several papers from her thesis.

Of greater interest here is that in 1993 Elena Raimúndez-Urrutia found bruchid beetles feeding in the seeds of *Vantanea minor* Benthham (Humiriaceae), one of the plants in her research on plant ecology (*i.e.*, reproductive efficiency of some plant species and the estimation of the reduction in the number of seeds produced due to the effect of predispersal seed predators; and host specificity of the insects) in the Gran Sabana of Venezuela. Because this species of bruchid was previously undescribed and the host and host family Humiriaceae had never been reported as a host for bruchids, we decided to collect more seeds and study the ecological interactions of the beetle and its host. Cibele S. Ribeiro-Costa (1999), who had earlier discovered the beetle as a new species in Brazil, described the beetle as *Amblycerus crassipunctatus* Ribeiro-Costa. For her new species description she used specimens from Brazil and from fruits collected in 1998 from the Gran Sabana of Venezuela by Raimúndez-Urrutia.

Amblycerus probably has the broadest range of hosts for any genus of bruchids. Species of *Amblycerus* have reliably been reported to feed in seeds of the Fabaceae, Malpighiaceae, Rhamnaceae, Boraginaceae, Combretaceae, Sterculiaceae, Tiliaceae, Vitaceae, Euphorbiaceae, and Anacardiaceae. Reports of feeding in seeds of Verbenaceae, Malvaceae, and Poaceae may be accurate and must be verified. With the addition of Humiriaceae as a host family, there are now 11 verified host families fed upon by species of *Amblycerus*. Host records for species of *Amblycerus* are scattered in the entomological literature but many are summarized in Romero *et al.* (1996). Other sources for hosts are papers discussed here and in Hetz and Johnson (1988), Johnson (1998), Kingsolver (1976, 1980), and Sharp (1885).

Results

The hostplant. The family Humiriaceae and the 14 to 16 species of *Vantanea* are primarily from South America but also occur in Panama and Costa Rica (Mabberley 1997). Species of *Vantanea* and the family Humiriaceae are shrubs or trees. In the Amazon, bats disperse fruits of species of *Vantanea* and *Humiria* but we know of no reports of bats feeding on fruits of *V. minor*. The size of the plant is dependent upon the area in which they grow. In the study area (see Host Records below), on sandy soil, *V. minor* is a shrub that may reach a height of 2 m and foliage diameter of 3 m. The average size is 1.5 m in height and 2 m in foliage diameter. In areas with more rainfall and thus moist soils, *V. minor* may become large trees. The mature fruit of *V. minor* (Figs. 1, 6) varies from 2.5 to 3.3 centimeters in diameter. The fruits persist on the plant for long periods of time. The fruits are almost impenetrable so they are most efficiently opened with a saw. The seeds are not as hard as the fruits, and have a high lipid content. Apparently, it is difficult for insects to

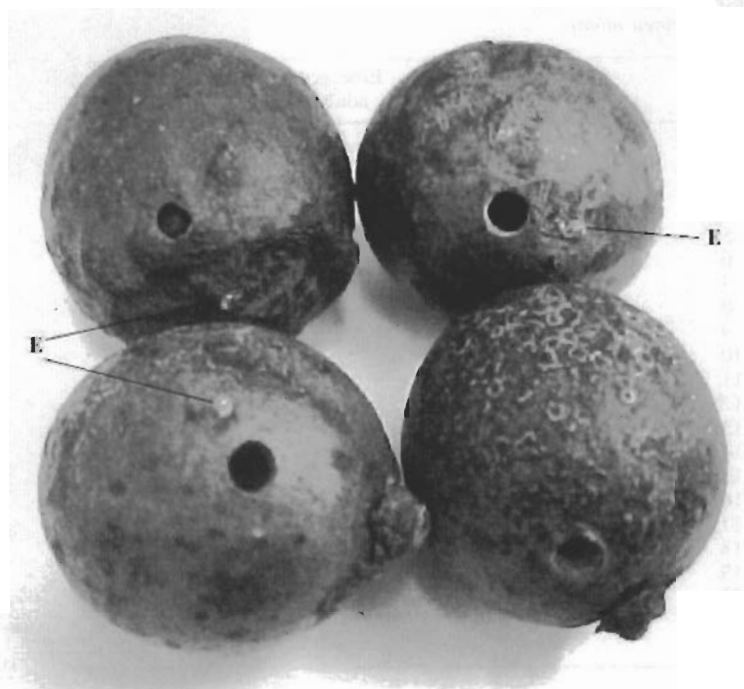


Fig. 1. Fruits of *Vantanea minor* with eggs (E) and exit holes of *Amblycerus crassipunctatus*.

enter and exit from these fruits because *Amblycerus crassipunctatus* is the only beetle that feeds in its seeds. (A species of Curculionidae, however, was found feeding in seeds of another species of Humiriaceae, *Humiria balsamifera* (Aubl.) St. Hil., by Raimúndez-Urrutia.)

Host Records for *A. crassipunctatus*: *Vantanea minor* Bentham: Venezuela: Bolivar: Arbustal Riworiwo, via Kavanayen, Gran Sabana, VIII-1993, E. Raimúndez, collector (2 specimens.); Shrub land near the Pemon (native people of the Gran Sabana) community of Iworiwo (also known as Liworiwo), 5°36.88'N–61°29.66'W, 1,208 m a. s. l., V-15-1998, E. Raimúndez, collector (7 specimens).

The insect. One of the problems with studying bruchid beetles is that they spend the major portion of their lives inside host seeds and fruits. Thus it is difficult to follow larval behavior and development. Special instruments and techniques must be used for these studies that are also very time consuming. An advantage of studying bruchid beetles is that it is relatively easy to associate the insects with their hosts if one has sufficient diligence to collect seeds and plants and to have the plants identified accurately. The insects must be carefully reared from the seeds and identified.

A sample of 21 fruits was collected in Venezuela and brought to the laboratory. We used ambient laboratory temperature for rearing the insects and the

Table 1. Number of eggs and exit holes of *Amblycerus crassipunctatus* on and in fruits of *Vantanea minor*.

Fruit number	Number of eggs/fruit	Emerged adults	% emerged adults
1	1	0	0
2	0	0	0
3	0	0	0
4	0	0	0
5	0	0	0
6	0	0	0
7	0	0	0
8	2	0	0
9	1	1	100
10	2	2	100
11	5	1	20
12	0	0	0
13	0	0	0
14	3	1	33.33
15	4	0	0
16	0	0	0
17	3	0	0
18	0	0	0
19	2	1	50
20	1	1	100
21	8	0	0
Total	32	7	21.87%

following results were obtained. More than half of the fruits (52.38%) had bruchid eggs glued to them (Table 1). The most eggs laid on a fruit was eight, and the most adults that emerged from one fruit was two. The eggs were oviposited on the surface of fruits, which places them in Guild A of Johnson (1981).

We counted the number of eggs laid on each fruit and then counted the number of adults that emerged from each fruit. The average number of adults that emerged per egg laid was 21.87% (Table 1). We considered that this average was probably low when compared with results that would be obtained under more controlled conditions and probably in nature. Examination of the eggs showed no evidence of mechanical damage or parasitism. We did find differences between hatched eggs and those not hatched. The eggs that hatched had dust that came from the hole drilled beneath the egg to provide entrance into the fruit. The eggs that did not hatch were transparent, and there was no sign of drilling beneath them, so these eggs may be infertile and could have been the reason for the low emergence. Another possibility was that the temperature and humidity were not ideal for them to thrive.

In this study of 21 fruits, six fruits (28.5%) had bruchid exit holes in them, so 28.5% of the fruits were damaged by *A. crassipunctatus*. In a separate study using 41 fruits, only 16 fruits (39%) contained seeds that had been fed upon by *A. crassipunctatus*.

Eggs of *A. crassipunctatus* are ovoid, 1.2 to 1.3 mm in length and 0.60 to 0.72 in width (Fig. 3). A flange surrounds eggs with glue on the periphery (Fig. 4). This is not unique to eggs of species of *Amblycerus* (Johnson and

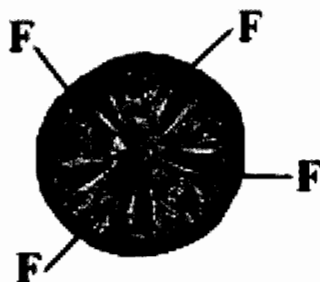


Fig. 2. Cross section through fruit of *Vantanea minor* showing seed cavities filled with frass (F) produced by *Amblycerus crassipunctatus*.

Kingsolver 1975), but may be common within the genus. The glue on the periphery of the flange that the female uses to attach the egg to the fruit is the only portion of the egg that is attached to the substrate. This makes eggs appear larger than they actually are. The size of the egg and flange together is 1.47 to 2.50 mm in length and 1.25 to 2.12 in width. The fringe area between the glue and the egg delimit an area that is not attached to the substrate. Eggs are therefore suspended above the surface of the substrate (see Johnson and Kingsolver 1975, Fig. 10). This kind of attachment may prevent the egg from becoming detached from the fruit as it matures and during eclosion of the first instar larva or protect eggs against mechanical injuries. Although eggs are most often laid singly, they are occasionally oviposited in clumps of two or three and occasionally overlap each other.

The first instar larva hatches, drills through the bottom of the egg, then drills into the fruit and then into a seed. The entry hole in the fruit is about 0.325 mm in diameter. Once inside the fruit, the larva feeds on seeds, leaving frass packed inside the cavities where the seeds developed (Fig. 2). If these larvae are similar to other bruchid larvae, they then develop through several instars, feeding as they grow. The last larval instar builds a thin, translucent cocoon inside the fruit and also makes a round, almost complete exit hole in the fruit wall leaving only a thin window of tissue in the wall. The larva then pupates inside its pupal chamber (Fig. 5). When an adult emerges from the fruit it pushes on the round window and exits. The exit hole is 2.6 to 3.5 mm in diameter (Fig. 6). The complete cycle is concluded in about two months.

Discussion

Janzen (1975) briefly and generally described the oviposition of *A. guazumicola* on fruits of *Guazuma ulmifolia*, and in his other papers (Janzen 1975, 1976, 1977, 1978, 1980) wrote general ecological accounts about bruchids including species of *Amblycerus*, but did not include detailed life history studies of these species.

There have been several life history studies of species of *Amblycerus*. Bondar (1931, 1932, 1937) discussed the life history of *A. nigromarginatus* (Motschulsky) in seeds of *Senna splendida* (Vog.) Irwin and Barneby; *A. dispar* (Sharp) (as *Spermophagus longissimus* (Pic)) in seeds of *Ziziphus joazeiro* Martius (Rhamnaceae); and *A. luteonotatus* (Pic) in seeds of an unknown species of Malpighiaceae with the common name of "trepadora lenhosa" (=

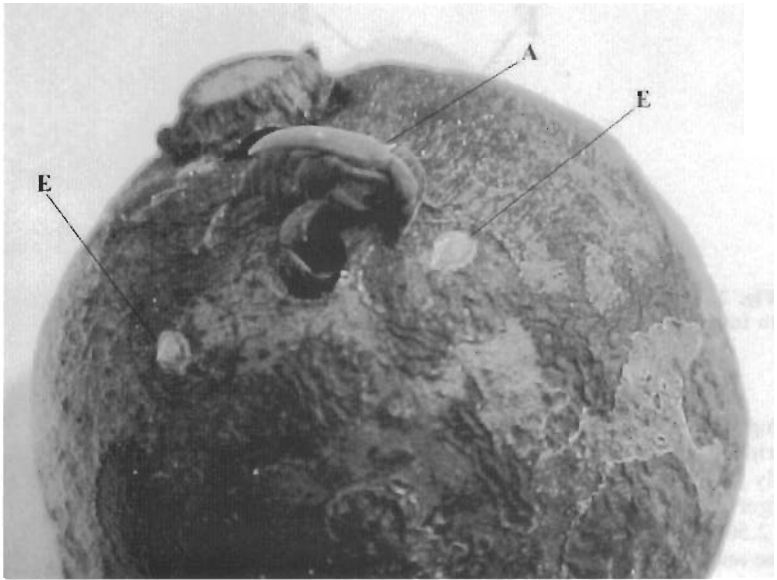


Fig. 3. Fruit of *Vantanea minor* with eggs (E) and adult (A) in exit hole of *Amblycerus crassipunctatus*.

woody climber). Johnson and Kingsolver (1971) published information on *A. guazumicola* Kingsolver and Johnson in seeds of *Guazuma ulmifolia* Lam. (Sterculiaceae) which they followed with a study of *A. vitis* (Schaeffer) in seeds of the Arizona grape *Vitis arizonica* Engelm. (Vitaceae) (Johnson and Kingsolver 1975). Pfaffenberger and Johnson (1976) then described briefly the life history of *A. acapulcensis* Kingsolver in seeds of *Caesalpinia cacalaco* Humb.

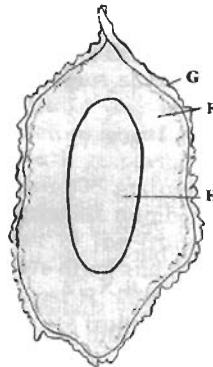


Fig. 4. Egg of *Amblycerus crassipunctatus* showing egg (E), flange (F) and peripheral glue (G).

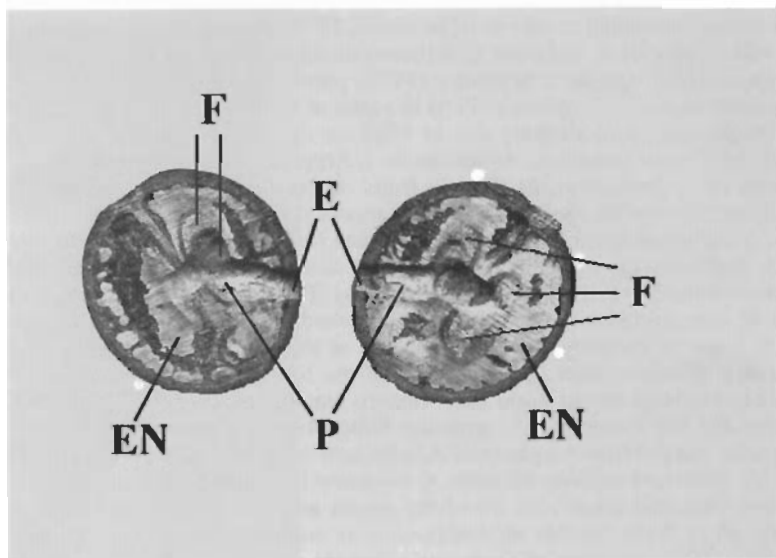


Fig. 5. Longitudinal section showing two halves of the same fruit of *Vantanea minor* with hard endocarpal tissue (EN); pupal chamber (P) lined with a thin, translucent membrane; frass-filled seed cavities (F); and exit hole (E) of *Amblycerus crassipunctatus*.

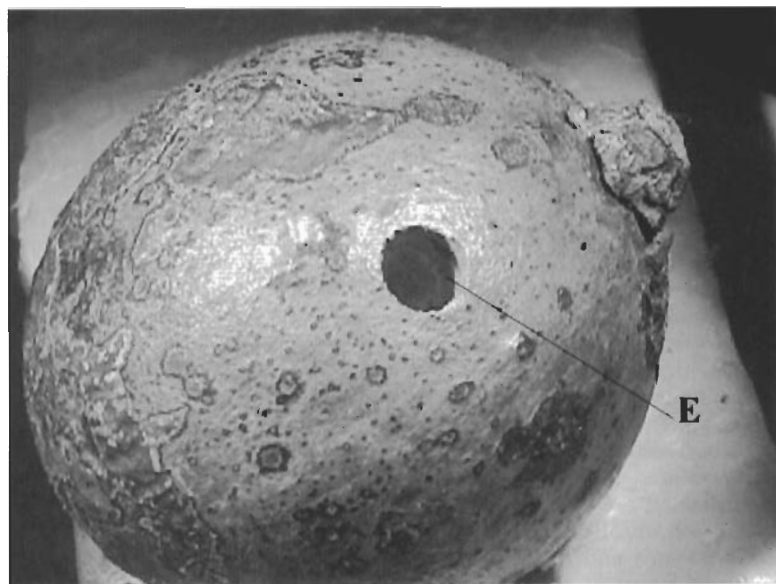


Fig. 6. Fruit of *Vantanea minor* with exit hole (E) of *Amblycerus crassipunctatus*.

and Bonpl. as related to larvae of bruchids. Pfaffenberger (1979) published on the life history of *A. robiniae* (Fabricius) in seeds of *Gleditsia triacanthos* L. Terán and Muruaga de L'Argentier (1979) published on the life history of *A. dispar* (as *A. caryoboriformis* (Pic)) in seeds of *Geoffroea decorticans* (Gillies ex Hook. and Arn.) Burkart and in 1981 on *A. hoffmanseggi* (Gyllenhal) in seeds of *Cassia hirsuta* L. Muruaga de L'Argentier (1983) described the life history of *A. longesuturalis* (Pic) in fruits of *Cordia trichotoma* (Vell.) Arráb. ex Steud. (Boraginaceae). Terán (1984) reported on *A. testaceus* (Pic) in seeds of *Cercidium australe* Johnst. Ribeiro-Costa (1992) discussed the life history of *A. hoffmanseggi* (Gyllenhal) in seeds of *Senna* cf. *bicapsularis* (L.) Roxb., compared the life history of *A. submaculatus* (Pic) in seeds *Senna bicapsularis* and *A. nigromarginatus* (Motschulsky) in seeds of *Senna corymbosa* (Lam.) H. S. Irwin & Barneby with the members of the Hoffmannseggi group of *Amblycerus*. Ribeiro-Costa (1998) published the life history of *A. submaculatus* (Pic) in seeds of *Senna alata* (L.). Genaro and Kingsolver (1997) briefly discussed the life history of *A. schwarzi* Kingsolver in fruits of *Terminalia catappa* L. and published a photo of *A. schwarzi* exit holes in the fruits. Mathwig (1972) discussed activity of adult *A. robiniae* in relation to their life history. Unless indicated otherwise, all of the plants are in the family Fabaceae. Because all of these species of *Amblycerus* as well as *A. cistelinus* (Gyllenhal) (Janzen 1975a) on fruits of *Guazuma ulmifolia* and *A. crassipunctatus* oviposit on fruits while they are on the tree, they are in Guild A of Johnson (1981).

Eggs and oviposition. Bondar (1931, 1932, 1937) described the oviposition of *A. dispar*, *A. luteonotatus* and *A. nigromarginatus* as being essentially the same for all three species: the eggs are oviposited one by one or in groups and are covered by a reticulate membrane. Terán (1984) reported a similar covering for the eggs of *A. testaceus* as did Ribeiro-Costa (1998) for *A. submaculatus*, Terán and Muruaga de L'Argentier (1981) and Ribeiro-Costa (1992) for *A. hoffmanseggi* and Terán and Muruaga de L'Argentier (1979) for *A. dispar*. These reticulate covering of eggs were not observed in *A. robiniae* (Pfaffenberger 1979), *A. acapulcensis* (Pfaffenberger and Johnson 1976), *A. longesuturalis* (Muruaga de L'Argentier 1983), or *A. crassipunctatus*. A flange surrounds eggs of *A. vitis*, *A. submaculatus*, *A. dispar*, *A. longesuturalis*, and *A. robiniae* with glue on the periphery similar to that of *A. crassipunctatus*. This kind of attachment may prevent the egg from becoming detached from the fruit as it matures and during eclosion of the first instar larva or protect eggs against mechanical injuries. We suspect that most, if not all, eggs of all of the species discussed have a similar flange with glue on the periphery, but the researchers cited here did not report this. The above authors reported that the location of placement of eggs on the fruit or seeds varied between and sometimes within species as some were clumped and others were laid singly. Also, some species oviposited on specific areas of the fruit or seed while most laid eggs in no observable pattern. Eggs were laid by *A. crassipunctatus* in no apparent pattern. Reports on the placement of eggs of most bruchids may be skewed because most species were observed in the lab where, in most bruchids, eggs tend to be laid in large numbers and placed on fruits and seeds indiscriminately.

Larval feeding. Bondar (1931, 1932, 1937) reported that the larvae of *A. nigromarginatus* and *A. luteonotatus* feed in several seeds in the course of their development as do *A. guazumicola* (Johnson and Kingsolver 1971); *A. testaceus* (Terán 1984); *A. hoffmanseggi* (Terán and Muruaga de L'Argentier 1981, Ribeiro-Costa 1992), and *A. submaculatus* (Ribeiro-Costa 1998). *A.*

crassipunctatus feeds on one to four or more seeds in the course of its development. In our limited study this species fed upon an average of two seeds. *A. longesuturalis* apparently feeds in only about one-half of one seed. *A. dispar* feeds in the single-seeded *Ziziphus joazeiro* (Bondar 1931, 1932, 1937). *A. vitis* (Johnson and Kingsolver 1975) feeds in only one seed inside a grape even when two or three seeds are available.

Pupae. The larvae of *A. nigromarginatus* build fibrous pupal chambers against the wall of the pod valve. When pupal development is completed, the adults emerge through the pod wall (Bondar 1931, 1932, 1937). Larvae of *A. guazumicola* and *A. cistelinus* spin a silken pupal chamber and the adults emerge through the wall of the fruit (Johnson and Kingsolver 1971; Janzen 1975a). *A. vitis* uses a single seed as a pupal chamber and the adult emerges through the wall of the fruit (Johnson and Kingsolver 1975). *A. robiniae* builds a silken pupal chamber inside the remnants of a seed and the adult emerges through the pod valve (Pfaffenberger 1979). The larvae of *A. testaceus* construct a thin, translucent cocoon that adheres to one or both internal walls of the pod and the adults emerge through the walls of the pod (Terán 1984). The larvae of *A. dispar* make a cocoon apparently made of detritus and the adults emerge through the fruit wall (Terán and Muruaga de L'Argentier 1979). Larvae of *A. hoffmanseggi* build a cocoon with a fibrous appearance and the adults emerge through the pod valve (Ribeiro-Costa 1992). The last instar larva of *A. submaculatus* spins a cocoon made of silk aggregated with frass and sometimes with destroyed seeds. The cocoon is cemented internally to the pod valves and the adults emerge through the pod valves (Ribeiro-Costa 1998). The larvae of *A. crassipunctatus* build a thin, translucent cocoon that lines the pupal chamber and the adults emerge through the fruit wall (Figs. 5-6).

Seed mortality. Only Janzen (1975a) has conducted intensive studies of seed mortality of a species of *Amblycerus*. He found that from 56% to 61% of fruits of *Guazuma ulmifolia* were attacked by *A. cistelinus*. Johnson and Kingsolver (1971) found that *A. guazumicola* damaged 25.6% of the seeds of *G. ulmifolia* in a much more limited study. Also in a limited study, Johnson and Kingsolver (1975) found that *A. vitis* fed upon about 1% of the fruits of *Vitis arizonica*. The percentage of fruits of *Geoffroea decorticans* attacked by *Amblycerus dispar* seems to oscillate between 20% to 25% (Terán and Muruaga de L'Argentier 1979). In our study of *A. crassipunctatus* damage to fruits of *V. minor*, we found that 28.5% to 39% of fruits were damaged. Except for the study by Janzen, this information is helpful but not very informative as to the degree of damage that these bruchids may inflict on seeds and thus the reproductive efficiency of their host plants. We exhort young biologists to conduct more studies on the ecology of bruchids and their hosts.

Thus, eggs of most species of *Amblycerus* have a reticulate covering and are probably surrounded by a flange with glue on the periphery. Placement of eggs on the fruit or seeds by females of *Amblycerus* varied sometimes within and usually between species as some were clumped and others were laid singly; some species oviposited on specific areas of the fruit or seed at various stages of their development while most laid eggs in no observable pattern. Eggs were laid by *A. crassipunctatus* in no apparent pattern. Reports on the placement of eggs of most bruchids may be biased because most species were observed in the lab where, in most bruchids, eggs tend to be laid in large numbers and placed on fruits and seeds indiscriminately.

Most larvae of *Amblycerus* species feed on several seeds during the course of their development. This, no doubt, has allowed them to evolve the large

size of the adults. Two species, *A. dispar* and *A. vitis*, feed in only one seed. We attribute this to the large size of seeds fed upon by *A. dispar*. Apparently, *A. vitis* has evolved a much smaller body size because it feeds in the small seeds of grapes. Arizona wild grapes usually have only one seed.

Apparently, almost all species of *Amblycerus* spin a cocoon for pupation. This was evolved probably because the large size of the adults not only led to the habit of feeding in several seeds and the cocoon provides protection during pupation. Most bruchids are much smaller in body size than species of *Amblycerus* and thus pupate inside a single seed, which negates the need for a cocoon. Because cocoons are spun attached to the fruit wall, the adults emerge through the wall.

It is interesting that *A. dispar* feeds in seeds of plants in the Rhamnaceae (*Ziziphus*) and the Fabaceae (*Geoffroea*). Because most species of bruchids usually feed in the same genera of host plants, these host preferences are very unusual.

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