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COMPARATIVE DESCRIPTION AND BIONOMICS OF THE FIRST AND FINAL LARVAL STAGES OF AMBLYCERUS ACAPULCENSIS KINGSOLVER AND A. ROBINIAE (FABRICIUS) (COLEOPTERA: BRUCHIDAE)

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The first and final larval instars of *Amblycerus acapulcensis* and *A. robiniae* are described and compared morphologically and ethologically. First instar characters used were those of the chaetotaxy, head, antennae, prothoracic plate, legs, spiracles, and anal sulcus. Final instar characters used were those of the antennae, clypeolabrum, epipharynx, mandibles, maxillae, labium, legs, spiracles, and anal sulcus. The ovum, ovipositional behavior, pupation, and post emergence activities are discussed.

Larvae of the seed weevils feed primarily within the seeds of leguminous plants. However, excepting a few economic forms, the activities of most bruchids remain unnoticed. The species discussed here are A. acapulcensis, which feeds mostly upon native Caesalpinia cacalaco Humb. and Bonpl., and A. robiniae, which feeds on native and/or cultivated varieties of Gleditsia triacanthos L.

Larval descriptions are of significance in revealing congruency or incongruency within the adult classification scheme. Moreover, additional information on ovipositional behavior, eggs, larval behavior, and pupation will provide substantial intra- and interfamilial phylogenetic clues.

Amblycerus acapulcensis Kingsolver

First instar described by Pfaffenberger and Johnson (1976).

Characteristics of the final instar. Body: (See Fig. 1 in Pfaffenberger 1977) length 5.0 to 7.0 mm, width 3.0 to 4.0 mm, C-shaped, robust; each succeeding thoracic segment increasing in diameter, metathoracic segment of greater width than 1st abdominal segment; first thru 5th abdominal segments subequal, segments 6-10 strongly tapered posteriorly; cuticle white or faintly yellow, thoracic pro-dorsum with lateral, comma-shaped, lightly pigmented, sclerotized areas; setae dense and conspicuous on sternopleural regions becoming sparse and inconspicuous over remainder of integument. Head: (See Figs. 3 and 4 in Pfaffenberger 1977) retracted, oval, dorso-ventrally flattened, ventral surface occupied mostly by occipital foramen; light tan coloration, pigmentation concentrated in and around mouthparts; single, pigmented ocellus near each antennal base, situated on opposite side of lyre-shaped epicranial suture. Antenna: (Fig. 1) located near base of mandible; 2 articulating, telescopic segments; basal segment retracting within tubular projection of head capsule; rectangular basal segment slightly shorter but wider than distal segment; apical end of rectangular, distal segment fringed peripherally with single row of narrow, elongate, sclerotized projections; projections surround single elongate seta and single sensilla basiconicum; setal length approximates that of distal segment while subtending sensillum is about 1/3 as long as seta. Clypeolabrum: (Fig. 2) lightly pigmented; clypeal portion horizontally rectangular with seta and proximomedial sensory pore located at extreme latero-medial edge; labral portion with



Final larval instar of *Amblycerus acapulcensis*: 1) antenna; 2) clypeolabrum; 3) epipharynx; 4) mandible; 5) maxilla; 6) labium; 7) leg; 8) spiracle.

convex, distal and flattened, proximal borders; clypeolabral suture overlapped by transversely, rectangular, pigmented area whose obtuse, lateral ends project proximo-medially; pigmented area supports short seta in each disto-lateral corner and one medial, elongate setal pair; single sensory pore located proximo-medial to each elongate seta; free border of labral portion covered with dense spinous mat. Epipharynx: (Fig. 3) biconvex, proximal region bearing pair of semiquadrate sclerotized plates; epipharyngeal groove bordered laterally by setal triad; medial pair short, broad, sometimes decurved, lateral seta longer and narrow; triad bisected by short, dense rows of spinous processes; distomedial margin with 6-crescentrically arranged, elongate blunt setae which may be concealed by dense spinous mat extending laterally along free distal margin. Mandible: (Fig. 4) prognathous, monocondylic, cutting surface concave, smooth molar surface. Maxilla: (Fig. 5) with crescent-shaped cardo bearing short, decurved seta at distal end, cardo pointed at both ends; stipes with blunt base, bearing 23 elongate setae on membranous region; palpifer bearing 5 setae in membranous region, 1 seta in sclerotized region approaching mala; palpus 2-segmented, basal segment flat with pair of setae and sensory pores in membranous region, setae located at opposite sides of distal palpal segment, apical end of distal segment with numerous basiconic sensillae; mala with 5 anteromedial, peg-shaped setae and 6 latero-ventral, stout, pointed setae. Hypopharynx: without sclerotized plates. Labium: (Fig. 6) submentum with lateral ends deflected anteriorly, ends nipple-shaped and bearing pair of short, sharp, medially located setae; two pairs of elongate setae located laterally in membranous region between submentum and mentum; mentum urn-shaped, bearing pair of small setae near base of prong-like anterior projections; glossae fused, supporting sensory pore and pair of setae at end of each projecting arm. Legs: (Fig. 7) distance between legs increasing with each succeeding segment, directed antero-medially; 3-segmented, 2nd segment bearing lateral and medial seta, basal segment with 1 postero-medial and 3 lateral setae; two sensory pores located along antero-proximal border of basal segment. Spiracles: (Fig. 8) uniforous, round, mesothoracic pair enlarged; atrial orifice with elaborate, sclerotized, branching projections, branches nearly obscuring underlying atrium; peritreme scale-like in appearance. Anus: Y-shaped, terminal.

Material Examined: 6 final instar larvae, Mexico. 6 mi N Los Mochis, Sinaloa, from seeds of *Caesalpinia cacalaco* Humb. and Bonpl., collected by C. D. Johnson. Determined by association with reared adults.

Amblycerus robiniae (Fabricius)

Characteristics of the first instar. Body: (See Fig. 1 in Pfaffenberger and Johnson 1976) length 1.0 mm, width 0.4 mm, width greatest in thoracic and 1st abdominal segments, remaining segments tapering to button-like 10th segment; cuticle white excepting prothoracic plate and sclerotized regions of appendages; Chaetotaxy similar to A. acapulcensis (Fig. 11 and 33 in Pfaffenberger and Johnson 1976). Head: as described for the adult of A. acapulcensis. Antenna: (Fig. 9) single segmented, rectangular, bearing large distal sensillum basiconicum, sensillum half as long as antennal segment; large, stout, seta, whose length exceeds length of antennal segment, emanating from distal third of segment. Prothoracic plate: (Fig. 10) (for terminology see Pfaffenberger and Johnson 1976) zygomorphic, median arms with 1 tooth, medial border of median arm confluent with same border of posterior arm with 6 teeth. Seta number 2 absent (see Fig. 22, J in Pfaffenberger and Johnson 1976), seta 1 and 3-5 aligned along antero-median aspects of plate. Anterior arms ending in oval patch of asperities which surround seta 1 and sensory pore, an additional sensory pore located between setae 1 and 3. Legs: (Fig. 11) 3-segmented, each pair longer than preceding pair; all segments bearing internal, flattened, sclerotized plate along anterior margin of segment; 3rd segment terminating in fleshy (possibly adhesive) lobe and opposable, C-shaped, sclerotized claw; 3 short setae encircle 3rd segment near end of internal sclerotized plate; 2nd segment with 1 medio-proximal and 2 medio-distal, short setae, 2 proximo-antero-lateral and 1 disto-postero-lateral sensory pores;



First instar larva of Amblycerus robiniae: 9) antenna; 10) prothoracic plate; 11) leg; 12) spiracle.

distal postero-lateral surface of 2nd segment bearing elongate, decurved seta. Spiracles: (Fig. 12) biforous, heart-shaped. Anus: Y-shaped, terminal.

Characteristics of the *final instar*. (Except where designated refer to description of A. acapulcensis). Antenna: (Fig. 13) apical end of distal segment with numerous, short, sharp projections subtending elongate seta and sensilla basiconicum. Clypeolabrum: (Fig. 14) sclerotized plate overlapping clypeolabral suture absent. Epipharynx: (Fig. 15) proximal portion with triangular, sclerotized plates. Maxilla: (Fig. 16) cardo triangular with broad, flat, distal end; stipes bearing 19-20 elongate setae on membranous region; palpifer with 4 setae in membranous region, plate of palpifer with 2 short, sharp, dorso-lateral setae; mala with 2 cone-shaped, 1 elongate, blunt and 4 elongate, pointed randomly arranged setae. Hypopharynx: (Fig. 17) with 2 obliquely arranged, rectangular-like, sclerotized plates. Labium: (Fig. 18) mentum quadrate with truncate base, mental setae located in deep, membranous clefts, anterior arms bearing pair of mediad sensory pores. Legs: (Fig. 19) segments 1 and 2 with heavy, internal, sclerotized plates along anterior margin, 2nd segment with distolateral seta. Spiracles: (Fig. 20) atrial orifice with few, sclerotized, nonbranched projections.



Final larval instar of *Amblycerus robiniae*: 13) antenna; 14) clypeolabrum; 15) epipharynx; 16) maxilla; 17) hypopharynx; 18) labium; 19) leg; 20) spiracle.

Material Examined: 14 first instar and 17 final instar larvae, campus of Eastern New Mexico University, from seeds of *Gleditsia triacanthos* L., collected by G. S. Pfaffenberger. Determined by association with reared adults.

DISCUSSION

Cursory examination of larvae indicates one rather than two species. Close affinities also appear among the adults (Kingsolver 1975). There are, however, some very basic and useful morphological differences. The most useful differences for the first stage larvae occur within the prothoracic plate and legs. Figure 22, J in Pfaffenberger and Johnson (1976) shows that each median arm of A. acapulcensis bears 2 rather than a single tooth (Fig. 10) and that actinomorphism prevails with respect to tooth number (8-9) on the posterior arms. A. robiniae bears a consistent, zygomorphic number of 6. The number of setae between the anterior arms also differs, with 5 pairs in A. acapulcensis and 4 pairs in A. robiniae. Leg characteristics of A. robiniae (Fig. 11) not found in A. acapulcensis (Fig. 23, J; Pfaffenberger and Johnson 1976) include the elongate seta at base of proximal segment, T-shaped internal sclerite and crescent-shaped sclerite of proximal and middle segments respectively, and the absence of setae along the anterior margin of the second segment.

The most useful features for distinguishing the final instar of A. robiniae include absence of peripheral, sclerotized projections on the distal antennal segment (Fig. 13), absence of sclerotized plate overlapping clypeolabral suture (Fig. 14), presence of epipharyngeal sclerites (Fig. 17) absence of a deep mental cleft in the labium (Fig. 18), presence of sclerites in the appendage (Fig. 19), and reduced number of spiracular projections (Fig. 20).

BIONOMICS

Oviposition: The pods of Gleditsia triacanthos L. (honey locust) are broad (2.5-3.5 cm), flat, and average 20-30 cm in length. When mature the succulent septal regions of immature pods become dry and hard. Dehydration precipitates dorso-ventral constriction, creating a sulcus between each of the serially arranged ovules. Females of A. robiniae appear to prefer these sulci as pod ovipositional sites. This species may also have retained the primitive random ovipositional behavior described for females of the genus Rhaebus (Luk'yanovich and Ter-Minasyan 1971). I found that A. robiniae may oviposit within leaf tissue along the leaflet margins (Fig. 21). This abnormal ovipositional behavior suggests the possible use of other non-traditional ovipositional sites such as ripe buds, flowers, and twigs. Such behavior has been observed and described for Rhaebus mannerheimi Motsch. by Luk'yanovich and Ter-Minasyan (1971).

The ova usually appear singly. However, on occasion the eggs may be clustered (3-14/cluster) as in Fig. 22, and/or randomly located over the pod integument (see *A. acapulcensis* in Pfaffenberger and Johnson 1976). Egg clustering may represent a form of parasitic deception in that most of the surface and peripheral eggs are non-viable. These 'decoys' appear black (Fig. 22) and may provide a shield of protection for the underlying viable ova against the braconid parasite *Urosigalphus bruchi* Crawford (Forister and Johnson 1971; Johnson and Kingsolver 1975).

Many seeds were recovered in an attempt to establish stock cultures.

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Fig. 21, (top) Possible first instar developmental chambers of A. robiniae, showing emergence holes, located along leaflet margins of host plant. Fig. 22, (bottom) Egg puddling of A. robiniae, showing central viable ovum flanked by two darkened "decoys".

The adults were placed in fruit jars containing several hundred seeds. Initially the females oviposited on the sides of the jar but within 3-4 weeks were ovipositing upon the seed surface. Of those eggs oviposited upon seeds the larvae consistently eclose through the venter of the egg and penetrate the underlying seed. One has to wonder how the larva deciphers the underlying substrate, which in effect determines dorsal or ventral eclosion.

Ovum: (1.2mm X 0.7mm) This is very similar to that of *Amblycerus vitis* (Schaeffer) as described by Johnson and Kingsolver (1975).

The semi-ovate ovum is concealed beneath a tough, membranous shield bearing hexagonal ridges (Fig. 22). This leathery shield bears a peripheral, adhesive flange and a surface membrane which acts to secure the ovum to a smooth, 'motile' pod surface. The elongate anterior tip which is found only on viable ova and not on 'decoys' (Fig. 22) appears to enhance surface adhesion. When the chorion was probed with forceps the adhesive flange would immediately give way. However, the anterior tip would remain secure, thus suspending the egg from the pod surface.

Eclosion: The anterior tip of the ovum appears to be associated with eclosion. For instance, larvae normally eclose upside down through the dorso-anterior region of the egg. In so doing, the larva assumes an erect position while facing the posterior pole of the egg. During the struggle for escape the larva would sway from side to side, and, as the body was twisted, the legs and elongate, abdominal setae were used to gain leverage. The resultant forces would act to dislodge the chorionic flange, thereby leaving the anterior chorionic extension as the only point of attachment. Hence, the larva was able to successfully eclose upon the pod surface. Is it possible that dorsal emergence and oviposition in sulci have been selected for by a weakened flange?

Larval behavior and pupation: Upon emergence, larval behavior is reminiscent of A. acapulcensis, as described by Pfaffenberger and Johnson (1976). Motility, in A. robiniae, was very much like a larval lepidopteran, that is, using the thoracic appendages to advance while the body was stabilized by the last abdominal segment. Thoracic appendages were then secured and the 10th segment was drawn forward. Motility in A. acapulcensis differed since the abdomen was not actively involved and movement was continuous, suggesting caraboid larval movement.

On occasion a larva would assume an erect posture while using the 10th (last) segment to secure itself, as in *A. acapulcensis* (Pfaffenberger and Johnson 1976). In that position, the elongate abdominal setae were important not only as sensory structures and in acquiring leverage but also in stabilizing the body as it was being frantically waved about.

Larvae became quite active when placed on the pod surface. One larva walked about 35 cm before it found a place in which to begin burrowing. The larva selected an interovular sulcus on the pod surface. This provided an excellent back drop for the larva which found it relatively easy to gain purchase. Its rapid penetration was enhanced by the additional gravitational force gained by attaching its 10th abdominal segment to a vertical portion of the pod valve. The dorsum was hunched, the primary setae were thrust outward as stabilizers, and the larva began to bore. While boring, the well developed legs were constantly repositioned to procure leverage. The fact that the legs remained attached, despite seemingly unusual force,

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makes one wonder whether or not a sticky substance may be exuded from the terminal lobe-like tarsal segment (Fig. 11).

Another larva began burrowing in a surface scar. This occurred following a 1.3 hour search for a suitable site. Burrowing by A. robiniae consumed about 30 minutes, much slower than in A. acapulcensis (about 5 minutes; Pfaffenberger and Johnson 1976). To overcome the time-associated risk factor, larvae may seek fissures or cracks in the pod surface. This became apparent when several pods were examined for entrance holes. No holes were found, yet numerous adults emerged from supposedly non-infested pods.

Burrowing larvae bore through the interovular septum and enter the ovular chamber from the same side. A space of approximately 3-4 mm exists between the locule wall and ovule surface. Therefore, once inside the locule, the larva likely relies heavily upon its elongate, sensory setae and erect, searching behavior to locate the ovule. With reference to the hilum, penetration was always in the distal 1/3 of the ovule and into the side which happened to rest against the locule wall, suggesting a need for added purchase.

Single larvae of A. robiniae and A. vitis (Johnson and Kingsolver 1975) develop within a single seed. According to Johnson and Kingsolver (1971) two larvae of A. guazumicola develop in each seed. Information for A. acapulcensis is not available. There is no indication of cannabilism among these species.

Upon penetrating the seed molting occurs, and the successive instars consume the entire contents of a seed. Prior to pupation the larva consumes, in addition to the cotyledons, most of the flattened areas of the seed integument on one or both sides. It does not prepare a weakened area in the pod coat for post-pupational emergence, as is seen in most bruchid species. Pupation most generally occurs within a ring-like remnant of the seed integument where the pupa receives protection by the walls of the indehiscent seed pod.

On several occasions, silken pupal chambers were constructed within the pod when only small integument fragments remained following larval feeding. In one experiment seeds were prematurely removed from the pods and placed in a jar. One larva continued feeding until its host seed was nearly devoured. It then began to construct its pupal chamber and in the process glued or attached several neighboring seeds together. When one of the seeds was removed the larva immediately began covering the hole with the silken material eventually forming a silken cocoon; such behavior resembles somewhat that of *Caryedon serratus* (01.) as described by Prevett (1967). The newly emerged adult appears to prepare and escape through the typical round exit holes in the pod wall.

Post emergence activities: According to Mathwig (1972), larvae, pupae, and adults may overwinter, and there appears to be bi-modal emergence during "early July and mid-October". Additional information concerning the bionomics of the A. robiniae adult may be obtained from this paper.

CONCLUDING REMARKS

The morphology and bionomics of the first and last larval stages of the two involved species provide substantial support for the existing adult

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classification scheme. Moreover, available information on ovipositional behavior, ovum, etc., of A. vitis and A. guazumicola (Johnson and Kingsolver 1975, 1971, respectively) indicates the existence of a well conceived, cohesive taxon.

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