

LIFE HISTORY AND MORPHOLOGY OF FIRST AND LAST  
LARVAL INSTARS OF COSTA RICAN  
*CARYEDES BRASILIENSIS* THUNBERG  
(COLEOPTERA: BRUCHIDAE)

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ABSTRACT

Life history of each of the stages of *Caryedes brasiliensis* Thunberg is discussed. First and final larval instars are described and photographed (SEM) and/or illustrated. Characters described are those of the body, head, antenna, clypeus, labrum, epipharynx, mandible, maxilla, labium, leg, spiracle, and anal sulcus. Larval sensillar structures are identified and functional descriptions are included in a discussion of larval behavior.

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*Caryedes brasiliensis* Thunberg is a large bruchid beetle that ranges from Costa Rica to Brazil (Kingsolver and Whitehead 1974) and preys on the seeds of *Dioclea* (Janzen 1971, 1980, 1984), a genus of large-seeded legume vines in the lowland neotropics. It is now understood that *C. brasiliensis* larvae can eat the contents of the canavanine-rich seeds of *Dioclea megacarpa* by having enzymes that can distinguish arginine from its potentially toxic non-protein amino acid analogue canavanine, and by being able to degrade canavanine and its degradation byproduct canaline into building blocks useful in protein synthesis (Rosenthal *et al.* 1976, 1977, 1978, 1982). It is not yet known whether these biochemical tricks are all or in part conducted by the beetle larva itself or by its microbial flora (G. A. Rosenthal, pers. comm.). Twelve years of field census of seed predation by *C. brasiliensis* in Costa Rica show that in almost every year, this beetle kills 50-99% of the *D. megacarpa* seed crop, has no larval parasitoids, and has no other larval host plants in deciduous forest habitats (Janzen 1980, 1984). This beetle is highly specialized to prey on the members of one genus of plants. Here, we describe the life history and morphology of the first and last instar larvae of *C. brasiliensis*.

Our goal is to further document the interaction of a particular seed predator with its host. We cannot as yet define the importance of the interaction of all the traits described, but we are confident that many of them have been evolutionarily molded by the interaction with *D. megacarpa*, or are traits evolved in other contexts, but that are now of importance to the interaction.

OVIPOSITION AND LARVAL DEVELOPMENT

In the dry deciduous forested lowlands of Guanacaste Province in northwestern Costa Rica, and more specifically in Santa Rosa National Park, 25 km

s. of La Cruz, oviposition occurs from October to January. These are the last two months of the 6-month rainy season and the first two of the dry season. The flowering of late July to early September produces fruits bearing rapidly filling seeds, the latter becoming full-sized by the season of oviposition. The beetle glues 20–40 eggs together to form an ootheca (Figs. 43–44) on the surface of the green fruit. The oothecae are usually formed on a fruit dehiscence suture or in a scar on the fruit surface (the scar being made by some other organism). We do not know how many oothecae a female can produce nor how many she produces in one oviposition bout. By the end of the oviposition season, a fruit may bear zero to several hundred oothecae. Causes of this variation are explored elsewhere (Janzen 1984).

A *D. megacarpa* fruit contains 1–5 seeds, and each seed is large enough for the development of 20–40 bruchids; the beetle adult size varies with the number in the seed. A seed usually weighs 6–14 g when mature and dormant, and is a 2–3 cm flattened ovoid sphere. At the time the bruchid larvae enter the seeds, the seeds are greater than full-sized and solidly filled. Both the seed coat and cotyledons are, however, still soft enough to puncture easily with a blunt wire. The seed coat is white at this time, and turns brown with hardening.

The first instar larvae leave the ootheca through a single hole in its center, where it is attached to the fruit epidermis. This hole is probably cut by the first larva to emerge; its sibs thus probably gain easy and direct access to a tunnel through the fruit wall. By following tunnels through fruit wall tissue, we have found that the larvae proceed through a single tunnel until they enter the cavity containing a seed. Some then mine through the seed coat and into the cotyledonary material, where they can develop to the pupal stage in 3–4 weeks. How many larvae, of the hundreds to thousands that enter a fruit, are successful in entering a seed is not clear. The journey from ootheca to seed can be through as little as 6 mm to as much as 4 cm of fruit wall tissues, depending on the geographic relationship of the ootheca to the seeds. Since it is commonplace for most but not all of the seeds in a fruit to be heavily attacked, with the remainder containing no bruchids (Janzen 1984), we suspect that differences in ease of penetration of fruit wall tissue result in spatial heterogeneity of attack within the fruit.

The fruit wall tissue is generally soft and parenchymatous, but certain areas are much richer in a clear to pink very tannin-rich resin that oozes out if the fruit wall is punctured or cut. This resin is absent from sutures in the fruit wall, and it is likely that is why oviposition is concentrated along the sutures. In the same context, severe wounding of the fruit wall results in an area somewhat covered with dry resin, but the tissue below exudes much less resin when punctured.

The tunnels through the fruit wall and the seed coat close up after the larvae pass through, so they are sealed into the fruit. However, the entrance holes through the fruit epidermis remain and can be counted when oothecae are removed.

Larval eclosion is synchronized over a 1–2 day period. Some cue from nature or the fruit signals this event weeks after the ootheca has been produced and days to weeks after the larvae are capable of exiting. The evidence for this is that if all the oothecae (of many ages) are stripped off a fruit before any larvae have begun to emerge from them (and several weeks before any will), many of the larvae will emerge from the oothecae the following day and nearly all will emerge within 2–5 days. These newly emerged larvae can be implanted in soft and full-sized seeds dissected out of the fruit; after punching a 1 mm

diameter hole through the seed coat with the wire of a two inch jumbo paper clip, the larvae are dropped into the hole head first.

To summarize, the challenges faced by the first instar larvae are drilling through moist and sometimes resin-rich fruit pulp, drilling through the moist, soft seed coat, and living in a cavity that is probably devoid of oxygen, in the soft to hard cotyledons.

There is no sign that developing larvae are cannibalistic. They often consume virtually all of the seed contents and may be found side by side if this is the case. Large beetles emerge from seeds with few larvae (but even here they may develop side by side), while smaller beetles come from seeds with the maximum number of larvae. Pupal cells are side by side or imbedded in unconsumed cotyledon, and thinly lined with silk and frass mix, with meconial material in the bottom. Before pupating, some of the individuals pupating in the external regions of the seed contents cut a circular groove almost all the way through the (now hard) seed coat. Upon emerging from the seed, some two months after the larva entered it, the adult beetle cuts more of the circular door away and pushes it out of the seed coat. Adults are trapped inside the semi-dehiscent fruit until it has opened enough to permit their exit (usually 3–5 mm between fruit valve margins, brought about by severe drying of the fruit late in the dry season (March–April)).

The recently emerged adult lives free in the habitat through the remainder of the dry season and all of the rainy season until fruits are available for oviposition in the next year's crop. In the late rainy season, adults are encountered feeding on nectar and pollen of the flowers of *Verbesina gigantea* (Compositae) and *Ardisia revoluta* (Myrsinaceae). There is only one generation of *C. brasiliensis* per year.

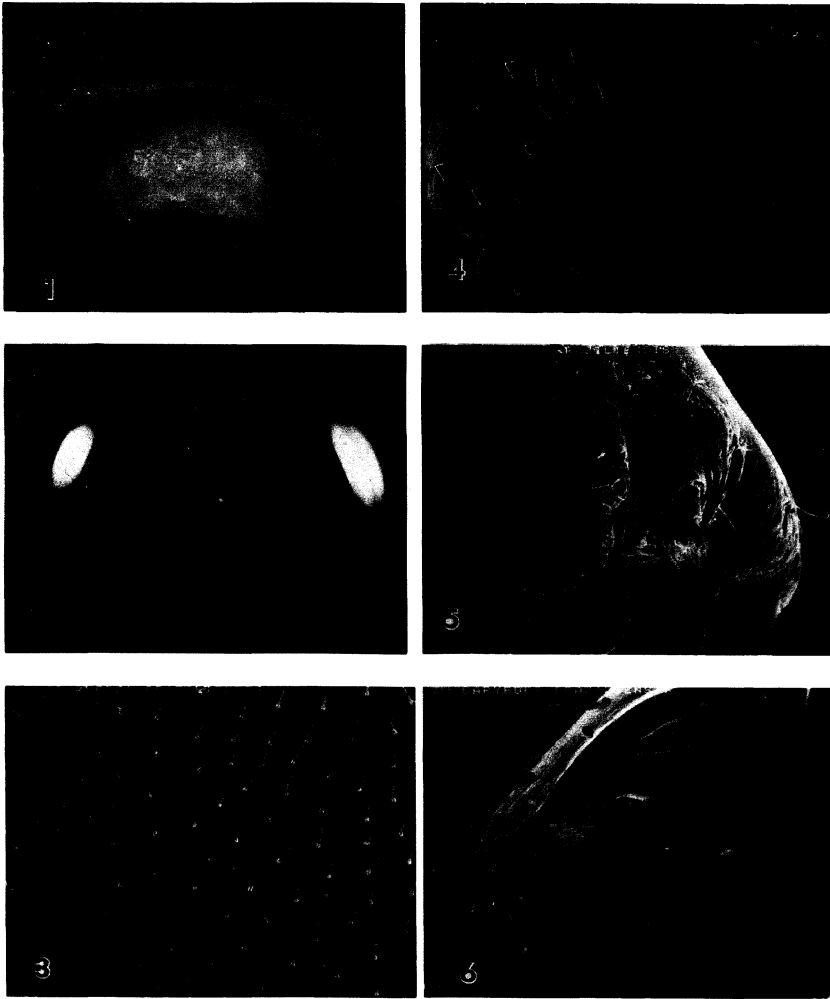
#### LARVAL PLIGHT

The challenges faced by the developing and last instar larvae are avoiding being eaten by other larvae, constructing a pupal cell, and cutting an exit hole almost through the hardening seed coat. They do all this while consuming food sufficiently rapidly that other larvae do not get it, and in an atmosphere probably poor in oxygen and rich in nitrogenous waste. Neither the seed nor inner fruit wall of *D. megacarpa* is chlorophyllous (Janzen 1983), and therefore it is unlikely that the seed coat has stomates or is very permeable to gasses.

It seems certain that the morphological traits of the larvae of *C. brasiliensis* figured and described in the following section are functional almost entirely in the context of the life history described above. For an insect, a bruchid larva leads a life uncomplicated morphologically and behaviorally (as is the case with other seed predators that live in seeds); it does, however, need a complex biochemistry that can not only perform normal insect metabolic activities, but also degrade or otherwise cope with the secondary compounds, such as canavanine, in the diet.

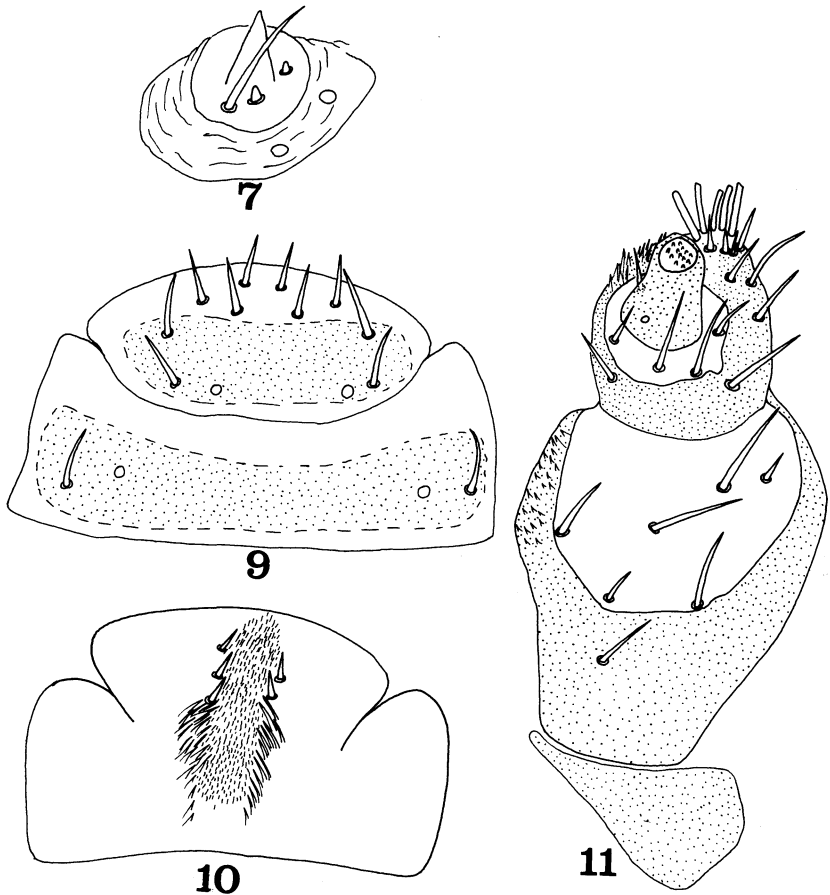
#### LARVAL MORPHOLOGY OF *CARYEDES BRASILIENSIS* THUNBERG

FINAL INSTAR. *Body* (Fig. 1). Length 8.0 mm, width 5.0 mm; color white to yellowish-white; pronotum (Fig. 2) with two dorsomedian, yellowish-brown, sclerotized areas; integument (Fig. 3) armed with dense mat of posteriorly decurved microtrichia. *Head* (Fig. 2). Retractable, oval shaped (Pfaffenberger 1977); Y-shaped epistomal suture terminating distally between antenna and ocellus at base of mandible (Fig. 4); color yellowish; deeply pigmented areas



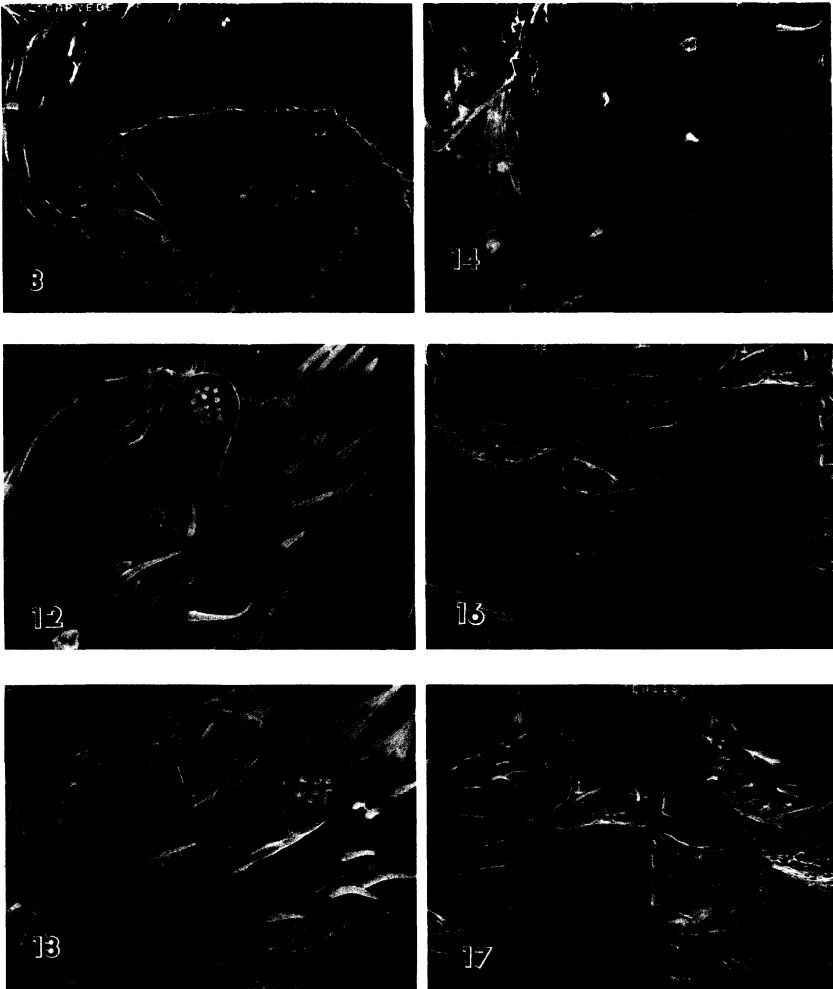
Figs. 1-6. *Caryedes brasiliensis*, final instar. 1, habitus. 2, head capsule and pronotum. 3, integument, dorsum. 4, frontal view of head capsule with chaetotaxy indicated by points. 5, lateral view of head capsule with ocellus indicated. 6, retractable, one-segmented antenna.

restricted to sclerites of mouthparts, mandibles and epistome (Fig. 2); pair of ocelli present (Fig. 5); chaetotaxy composed of nine pairs of sensilla (Fig. 5). *Antenna* (Figs. 6-7). One-segmented; retractable; sclerite only vaguely sclerotized; distal end with peripheral fringe of microtrichia; central area of distal end (Fig. 7) occupied by enlarged sensillum basiconicum subtended, laterally and dorsally, by pair of sensilla coeloconica, an elongate sensillum trichodeum located dorsad of basiconicum base; 3 sensory pores subtend antennal segment,



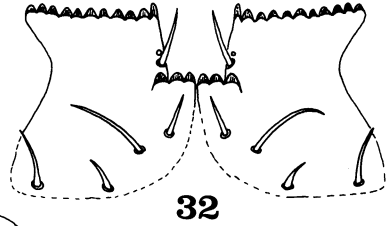
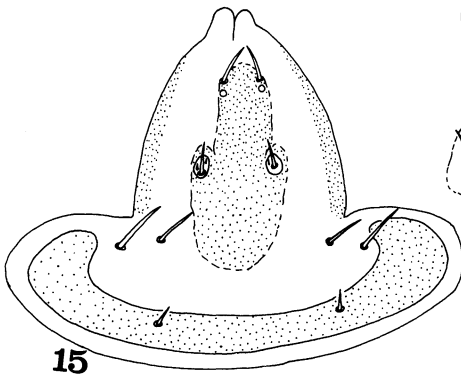
Figs. 7, 9–11. *Caryedes brasiliensis*, final instar. 7, antenna with sensory structures, microtrichia not shown. 9, sensilla on clypeolabrum, labral fringe of microtrichia not shown. 10, epipharynx. 11, maxilla with cardo.

1 dorsal, 1 lateral, and 1 ventral. *Clypeus* (Figs. 8–9). Quadrate base, concave distal margin; trichoid sensillum and subtending sensory pore located laterally; sclerite basically rectangular-shaped. *Labrum* (Figs. 8–9). Oval-shaped; bearing 10 sensilla trichodea and 2 sensory pores interspersed among dense mat of macrotrichia (Fig. 8); 4 sensilla trichodea form a linear arc near distal margin while remaining sensilla and sensory pores are in a reversed C arrangement; sclerite elongate to oval. *Epipharynx* (Fig. 10). Epipharyngeal groove lined with dense mat of minute microtrichia; groove bordered proximally by margins of macrotrichia and distally by sensilla trichodea; if equal numbers of trichoid sensilla exist there are 2 pairs present (however, the right side generally has 1 more sensillum than the left, e.g., 3 on right and 2 on left or 2 on right and 1 on left). *Mandible* (Fig. 4). Monocondylic, bearing 2 sensilla trichodea on



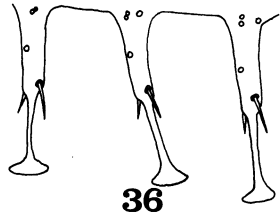
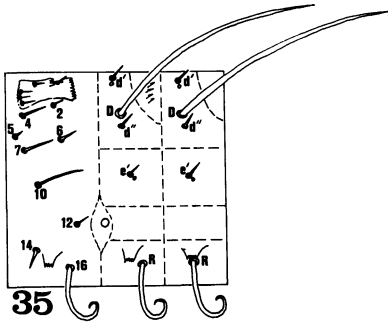
Figs. 8, 12-14, 16-17. *Caryedes brasiliensis*, final instar. 8, Clypeolabrum. 12, maxillary palpifer and palp. 13, maxillary palp with unique sensillum placodeum. 14, chaetotaxy of maxillary stipes; pointed sensillum occurs on sclerite. 16, labial mentum and paired sensilla to the lower left of mentum. 17, labial mental and premental chaetotaxy.

anterodorsal surface. *Maxilla* (Figs. 11-14). Cardio present (Fig. 11), triangular shaped; stipital sclerite bearing 1 trichoid sensillum (Figs. 11, 14) and numerous microtrichia on mandibular surface; membranous area with 3-6, but more generally with 4 sensilla trichodea; palpifer bearing 11-13 sensilla trichodea plus 5 articulated, spatulate-shaped to pointed setae, mandibular surface bearing many microtrichia (Figs. 11-13); palpus with lateral sensory pore near base; apex of palpus with 13 sensilla basiconica; lateral surface of palpus bearing a



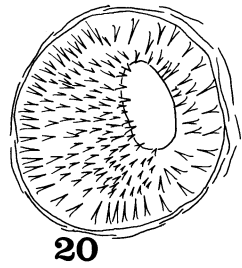
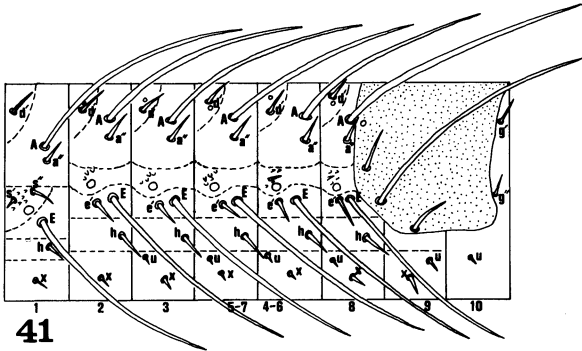
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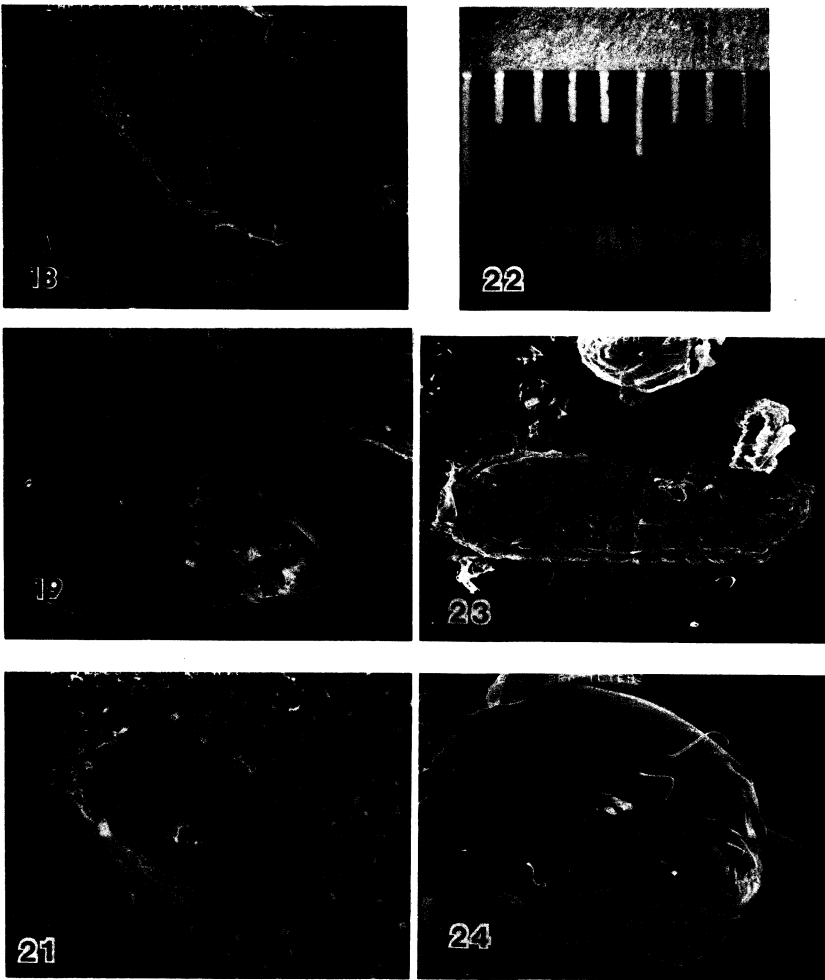


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Figs. 15, 20, 32, 35-36, 41. *Caryedes brasiliensis*. 15, labium, final instar. 20, atrial armature of abdominal spiracle, final instar. 32, prothoracic plate, first instar. 36, chaetotaxy and sensory pores of appendages, first instar. 35, Thoracic chaetotaxy, first instar. 41, Abdominal chaetotaxy, first instar.

unique sensillum placodeum (see Addendum). *Labium* (Figs. 15-17). Submentum 'C' or canoe-shaped, bearing 2 secondary sensilla trichodea; mentum with 2 pairs of trichoid sensilla in proximolateral, membranous areas (Figs. 15-16), sclerite basically oval bearing 2 pairs of trichoid sensilla, 1 pair me-



Figs. 18–19, 21–24. *Caryedes brasiliensis*. 18, prothoracic and mesothoracic sterna showing bulbous appendage, final instar. 19, chaetotaxy of bulbous appendage, final instar. 21, spiracle, final instar. 22, dimensions, first instar. 23, venter, first instar. 24, lateral view of head capsule with indicated ocellus.

diolateral, and 1 distal pair, latter subtended by sensory pore; mediolateral pair isolated in membranous islets and subtended by 1 or 2 minute microtrichia; mental sclerite bordered laterally by elongate sclerotic margins (Figs. 15–17). *Leg* (Figs. 18–19). One-segmented; retractable lobes bearing 2 distal trichoid sensilla and numerous sensory pores. *Spiracle* (Figs. 20–21). Spherical; thoracic pair enlarged; atrial orifice lined with microtrichia. *Anal sulcus*. Y-shaped.

**FIRST INSTAR.** *Body* (Figs. 22–23; see also Fig. 1 in Pfaffenberger and Johnson 1976). Length 1.2 mm, width 0.4 mm; sides parallel; greatest depth among



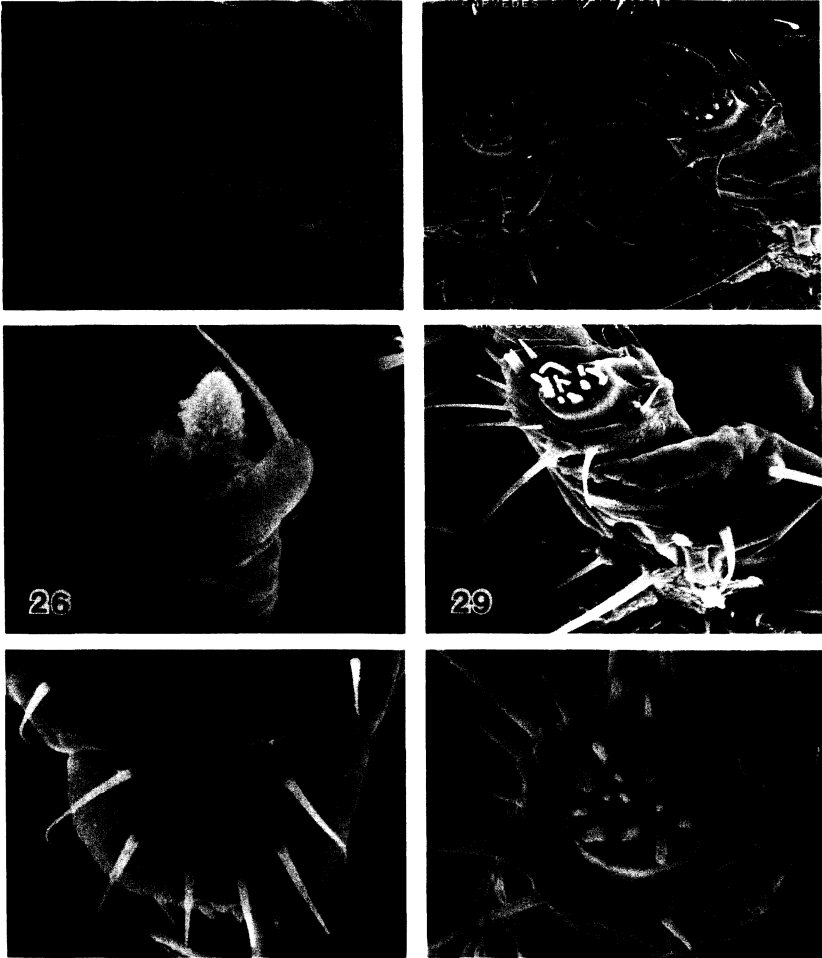
Table 1. Distribution of setae on *Caryedes brasiliensis*, first instar.

Segment	Pro-dorsum	Post-dorsum	Spiracular area	Epi-pleuron	Hypo-pleuron	Sternum	Prothorax
Mesothorax	Dd' d''			e'		R	2
Metathorax	Dd' d''			e'		R	4
Abdomen							5
1	d'	A a''	s' s''	E	h	x	6
2	d'	A a''		Ee'	h	x	7
3	d'	A a''		Ee'	h	u x	10
4 and 6	d'	A a''	*	Ee'	h	u x	12
5 and 7	d'	A a''		Ee'	h	u x	14
8	d'	A a''		Ee'	h	u x	16
9**						u x	
10 g' g''						u	

\* With single microtrichia.

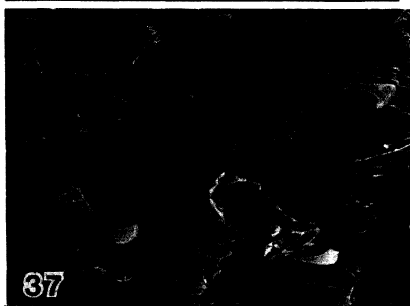
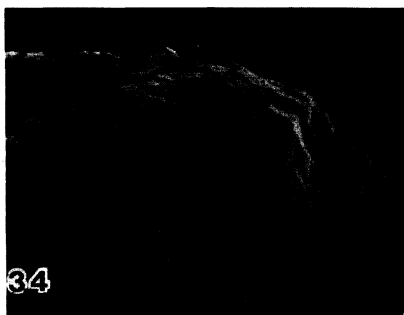
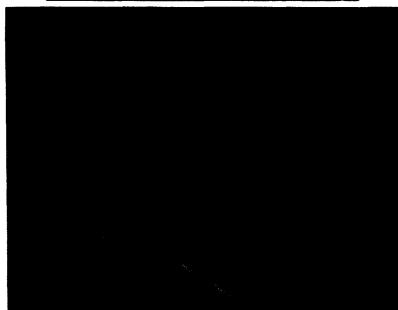
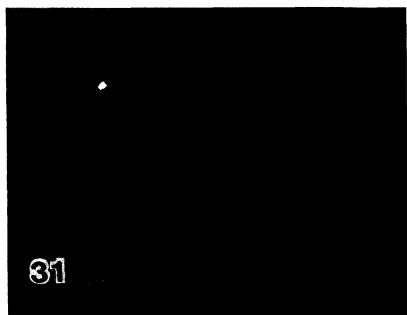
\*\* Dorsum covered with plate.

mesothoracic through 2nd abdominal segments; integument white except for pigmented prothoracic plate and portions of head capsule. *Head* (Figs. 24–25). Retractable; prognathous to hypognathous; bearing 7 pairs of trichoid sensilla; forks of Y-shaped epistomal suture ending near proximoventral margin of mandibles, single ocellus immediately posterior to this junction. *Antenna* (Fig. 26). One-segmented; retractable; apical end bearing medial sensillum chaeticum, enlarged, ventromedial sensillum coeloconicum and 2 smaller coeloconic sensilla, 1 at lateral base of sensillum chaeticum and the other lateral to coeloconic sensillum. *Clypeolabrum* (Figs. 25, 27). Clypeal portion rectangular in shape; labral portion U-shaped; chaetotaxy similar to final instar; distal arc of 4 trichoid sensilla deflected posteroventrally. *Mandible* (Fig. 24). Articulation and chaetotaxy similar to final instar. *Maxilla* (Figs. 28–30). Similar to that of final instar except 11 trichoid sensilla present on palpifer; macrotrichia clustered near lateral aspects of mandibular margin. *Labium* (Figs. 28, 31). Similar to that of final instar; sclerotization uncertain. *Prothoracic plate* (Figs. 32–34). H-shaped; basically quadrate in appearance; median arms absent; numbers of teeth per anterior and posterior arms variable; anterior arms with a 3-2, 2-3 or 3-3 tooth arrangement, with 3-3 being the most common; numbers of teeth on posterior arms (right half number appears first) may be 8-9, 10-10, 11-11 or 11-12, with the latter two arrangements being the most common; medial tooth (occasionally 2nd tooth) of posterior arms, normally elongate; 5 pairs of trichoid sensilla and pair of sensory pores present; sensilla along proximal margin alternately secondary (short) and primary (long); plate bordered laterally and posteriorly by mat of posteriorly pointed, integumental projections (Figs. 34, 36). *Prothorax* (Figs. 35–36). Bearing 9 trichoid sensilla in addition to those appearing on plate (Fig. 35); mats of posteriorly directed, integumental projections evident in Fig. 36. *Mesothorax* and *Metathorax* (Fig. 35). Chaetotaxy similar; prodorsa with primary (D) and 2 secondary (d' d'') sensilla; sensillum d' subtended by sensory pore; mesothoracic postdorsum with several, posteriorly directed, integumental projections; epipleura with single secondary (e') sensillum and subtending sensory pore; hypopleura aseptiferous; spiracle at hypopleural level between pro- and mesothorax; sterna (Figs. 23, 35, 37) bearing



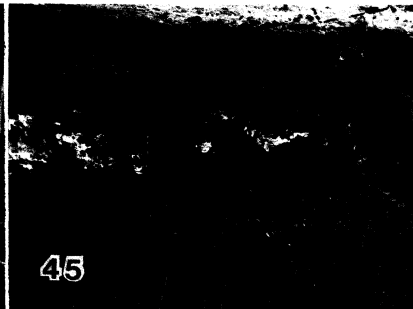
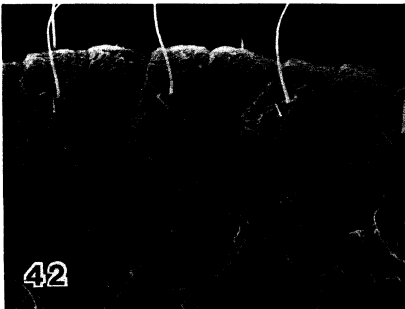
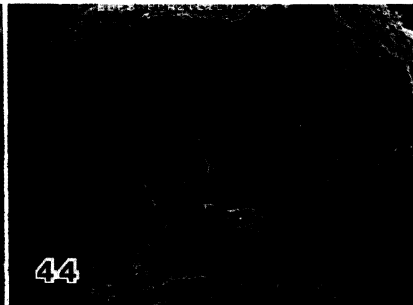
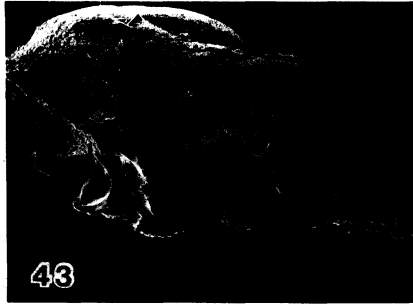
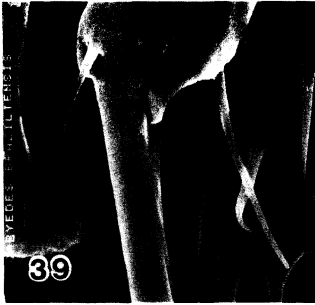
Figs. 25–30. *Caryedes brasiliensis*, first instar. 25, frontal view of head capsule. 26, one-segmented antenna. 27, clypeolabrum. 28, maxillae and labium. 29, maxilla. 30, maxillary palpifer and palp with indicated unique sensillum placodeum.

pair of elongate, distally coiled, trichoid sensilla (R); remainder of sternal surface with dense cover of posteriorly directed microtrichia. *Legs* (Figs. 36–39). Each succeeding pair slightly longer than previous pair, and with greater transverse, interpodal distance; 2 segmented; basal segment with either 2 (prothoracic appendage) or 3 (meso-metathoracic segments) basal sensory pores, 1 median sensory pore, 1 distal, posterolateral trichoid sensillum and 1 distal anteromedial microtrichia; apical end of distal segment expanded laterally. *Spiracle* (Figs. 35, 40–42). Spherical; orifice slit-like, covered with flexible extensions of integument. *Abdomen* (Figs. 41–42). Prodorsa with single, sec-



Figs. 31, 33–34, 36–38. *Caryedes brasiliensis*, first instar. 31, labial chaetotaxy, indicating submental sensillum. 33, anterodorsal view of prothoracic plate. 34, lateral view of prothoracic plate. 36, lateral view of head capsule and prothorax, showing posteriorly directed, integumental projections. 37, legs in reflexed position; note dense mat of microtrichia and sensillum R (see Fig. 35). 38, legs in extended position.

ondary sensillum (d'), sensillum on segments 2–8 with subtending sensory pore, pore dorsad to sensillum on segments 2–6 and ventrad to sensillum on segments 5–8; postdorsa with single primary (A) and secondary (a'') sensilla; dorsum of 9th, 10th, and part of 8th segments covered with enlarged, sclerotized plate, plate bearing medial sensory pore, 2 secondary sensilla which are separated by



Figs. 39–40, 42–45. *Caryedes brasiliensis*, first instar. 39, joint between first and second segments of leg. 40, spiracle. 42, first (on right) through fourth (on left) abdominal segments showing prodorsal, postdorsal, spiracular, epipleural and hypopleural regions with associated chaetotaxy (compare with Fig. 41). 43, clustered egg mass indicating hyaline area through which dorsal emergence may occur. 44, ventral view of egg mass showing ventral emergence holes. 45, cross-sectional view of pod coat.

elongate primary sensillum, all structures appear along anterolateral margins of plate; integumental nodules (some pointed) appear on all tergal and spiracular areas, but appear more frequently on the prodorsa. Spiracular areas 2–3, 5, 7, and 8 with nodules only; segments 1, 4, and 6 with microtrichial spine and nodules; 1st epipleurite with single (E) primary sensillum, epipleurites 2–8 with single primary (E) and secondary (e) sensilla; hypopleura 2–8 with single secondary (h) sensillum (Fig. 42); 1st and 2nd sternites with single (x) trichoid sensillum, sternites 3–9 with 2 (u, x) sensilla, all sensilla found among dense mat of microtrichia (Figs. 23, 37–39); 10th segment bearing 3 secondary (g', g'' and u) sensilla. *Anal sulcus*. Y-shaped.

EGG (Figs. 43–44). Eggs are deposited in pooled masses (oothecae) upon the surface of the fruit. All eggs, however, are vertically arranged and parallel to one another within the egg mass. As indicated earlier, emergence is ventral (Fig. 44) which enables the first instar to use the ootheca as leverage during pod penetration.

SIGNIFICANT CHARACTERS. *Final instar*. Single pair of ocelli; one-segmented antenna whose end is occupied by 1 basiconic, 2 coeloconic, and 1 trichoid sensilla; presence of 10 trichoid sensilla on oval-shaped labrum; epipharyngeal groove lined with minute microtrichia and bordered by an even or uneven number of trichoid sensilla (if uneven sensilla exist then right side will have one more sensillum than left side); 3–6 (average number of 4) trichoid sensilla present on stipes; 11–13 trichoid sensilla present on palpifer, these in addition to the 5 pairs of food manipulating, spatulate-shaped sensilla; maxillary palp bearing 13 terminal, sensilla basiconica; oval-shaped mental sclerite; one-segmented leg bearing a pair of trichoid sensilla; atrial orifice of spiracle lined with microtrichia; Y-shaped anal sulcus. *First instar*. Single pair of ocelli; diversity and arrangement of antennal, sensillar structures; maxillary palpifer with 11 trichoid sensilla; uneven numbers of teeth on anterior and posterior arms of prothoracic plate, 5 pairs of sensilla associated with the plate; elongate median tooth on posterior arms of plate; prothorax with 9 sensilla and mats of integumental projections; presence of sensilla Dd'd' on meso-metathoracic prodorsa and sensillum e' on the same epipleurites; slit-like spiracular orifice; nodules and microtrichial spines on spiracular areas; presence of sclerotized plate covering dorsum of 9th, 10th, and parts of 8th segments. *Egg*. Vertical and parallel arrangement of eggs within the ootheca.

MATERIAL EXAMINED. Descriptions based on 31 final instar larvae and 57 first instar larvae. Collected from fruits of *Dioclea megacarpa*, December 1982, Parque Nacional Santa Rosa, 25 km s. of LaCruz, Guanacaste Province, Costa Rica, D. H. Janzen collector. Taxonomic identity determined by host plant association and by reared adults.

#### DISCUSSION

Bruchids are not well known neurophysiologically (Pouzat 1981), therefore much of our functional interpretation is based upon current knowledge of sensillar structures (McIver 1982). Aside from ocelli, *C. brasiliensis* larvae also possess other sensory receptors which enable them to perceive their surroundings. These receptors and associated functions include: *sensilla basiconica* (Figs. 26, 30) which function in olfaction and contact chemoreception (antenna and maxilla; McIver 1982; Pouzat 1981), *sensilla coeloconica* (Fig. 26) which are sensitive to odors (antennae; McIver 1982), *sensilla chaetica* (Fig. 26) which function in mechanoreception (antennae; McIver 1982), *sensilla trichodea* (Figs. 27–28) which are used in the olfaction of repellents and attractants (head, mouthparts, legs, and body; McIver 1982), and *sensory pores* (olfaction). McIver (1982) also observed functional differences between types of trichoid sensillae. For example, impulse frequency increased among the pointed forms (Figs. 25, 28, 31) when exposed to fatty acids and essential plant oils while natural repellents reduced impulses in the same sensillae. The blunt tipped forms (Figs. 28–30), however, were found to be sensitive to fatty acids of varying lengths (shorter chains reducing and longer chains increasing impulse frequency).

We are not in a position to ascribe unequivocal evidence of function for the varying morphological features of *C. brasiliensis* larvae. There are questions, however, regarding functional morphology to which responses can be made, such as: (1) How does the larva know which way to drill to start into the fruit

from the egg? (2) Once inside the fruit wall, how is it able to direct itself toward the seed? (3) How is the larva able to seek out a previously drilled tunnel? (4) Once in the lacuna containing the seed, how is the larva able to gain the leverage necessary to penetrate the smooth seed surface? (5) While in the seed, how is the larva able to recognize a neighboring cavity occupied by another larva? (6) During the latter stages of larval development, how is the larva able to recognize the seed coat so that it can initiate excavation for adult emergence?

With the foregoing sensillar functions in mind and in response to questions regarding larval behavior, we are now able to establish probable cause and effect relationships. In answer to our first question, we suspect that the larva gravitates toward the oothecal-fruit interface in response to reduction in light intensity. As can be seen in Figure 43, the oothecal membrane is hyaline-like and is therefore easily penetrated by light waves. The larva being able to perceive light waves, with its ocelli (Fig. 24), would then respond in a photonegative way by seeking darker areas, thus moving toward the oothecal-fruit interface.

Our second question is best answered by examining Figure 45. Shown is a cross-section of the outer pod wall, which reveals the presence of multiple layers, each differing in texture and consistency and perhaps even chemically. The first instar may possess an innate awareness of the textural and chemical sequences through which it must pass before reaching the lacuna containing the seed. The differences in layers ('layer effect') of the fruit coat are probably perceived by all sensillar structures mentioned above.

The larva could probably locate a previously drilled tunnel (question three) by either sensing the odor of frass from previous occupants (sensilla coeloconica on each antenna) or perhaps by detecting gnawing vibrations of other larvae (sensilla chaetica on antennae).

A response to question four is less obvious, but could partially explain the presence of the heavily sclerotized plate (Figs. 23, 41), which overlies abdominal segments 8-10. The distance between the lacunar wall and that of the ovule is substantial and therefore would prevent the larva from gaining leverage sufficient to penetrate the seed coat. Once the larva entered the lacunar cavity it would simply use its mechanoreceptors (sensilla chaetica on the antennae and possibly proprioceptors such as those at the posterior angle of the distal leg joint; Fig. 39) to locate the point where the seed was at rest upon the lacunar wall. Subsequent activities would likely involve the use of the anal aperture and primary abdominal setae (Pfaffenberger 1979; Pfaffenberger and Johnson 1976) as well as the enlarged abdominal plate. The plate undoubtedly provides invaluable muscle attachment surface area for gaining added purchase and would likely add stability to the erect body during the drilling process. Once the prothorax has penetrated the seed coat the larva would gain added purchase by utilizing the prothoracic plate and the sclerotized, posteriorly directed, projections (Figs. 34, 36).

The sensilla chaetica and *s. coeloconica* would once again (question five) be used to detect a neighboring larva by its gnawing vibrations and frass odors, respectively. As the strength of odors and vibrations from neighboring larvae increased, the larva would simply concentrate more of its excavating efforts in other areas of its chamber, thus avoiding or reducing contact.

As the final larval instar approached pupation (question six), innate compulsion would probably cause it to once again become sensitive to the seed coat contents (sensilla basiconica, sensilla trichodea, sensory pores and sensilla coeloconica; Figs. 8-19), this time merely to gnaw, rather than eat, as it carves the emergence hole for its imaginal stage. The larva is stopped short of gnawing completely through the seed coat by either the 'layer effect' (see above), by

changes in vibration properties of the thinning seed coat, by penetrating light waves which it could perceive with its ocelli (Fig. 5), or perhaps by combinations of these.

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## ADDENDUM

Unfortunately during the preparation of this paper, an important paper was overlooked [Richerson, J. V., J. H. Borden, and J. Hollingdale. 1947. Morphology of a unique sensillum placodeum on the antennae of *Coeloides brunneri* (Hymenoptera: Braconidae). *Can. Jour. Zool.* 50:909-913]. These authors noted that the ultrastructure of the unique sensillum placodeum "does not support a chemoreceptor or other function, but does provide considerable evidence to support an infrared radiation receptor function."