

A NOVEL ORGAN AND MECHANISM FOR LARVAL SOUND PRODUCTION IN BUTTERFLY CATERPILLARS: *EURYBIA ELVINA* (LEPIDOPTERA: RIODINIDAE)*

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Abstract – *Eurybia elvina* larvae produce substrate-borne vibrations by grating a cervical membrane studded with teeth against hemispherical protuberances scattered along the surface of the head.

Key words: *Alesa*, ants, *Arhopala*, behavior, Central America, Eurybiini, Formicidae, hostplants, Hymenoptera, immature stages, *Jalmenus*, larvae, larval behavior, Lemoniadini, life history, Lycaenidae, Marantaceae, *Mimocastnia*, Mesoamerica, morphology, myrmecophily, Neotropical, Nymphidiini, Panama.

In a survey of sound production in butterfly caterpillars, DeVries (1990, 1991; DeVries *et al.*, 1994) found that only those butterflies in the families Lycaenidae and Riodinidae that associate with ants produce substrate-borne sounds. Among the riodinids these include members of the tribes Lemoniadini, Nymphidiini, and Eurybiini (*sensu* Harvey, 1987, but see Penz and DeVries, 1999). Lemoniine and nymphidiine larvae produce sound with vibratory papillae, minute rod-like appendages that project over the head from the anterior margin of the prothorax. To call, the vibratory papillae rapidly strike the dorsum of the head, which oscillates in an anterior-posterior direction, allowing microscopic bumps on its surface, called epicranial granulations, to work their way between a papilla's grooves, thereby producing a vibrational signal. Given the experimental evidence that muted caterpillars of *Thisbe irenea* (Stoll) (Riodinidae) attracted fewer attendant ants than did those that could produce calls and, moreover, the widespread ability of myrmecophilous caterpillars to call, DeVries (1990, 1991, 1997) concluded that sound production is important in butterfly-ant

interactions.

Riodinid larvae in the tribe Eurybiini also produce sound: DeVries (1991) described calls by members of the genus *Eurybia* as trains of “eh-eh-eh-eh . . .” with 12-15 pulses produced per second. However, the organ and mechanism of sound production have hitherto been unknown. Caterpillars in the genus *Eurybia* lack vibratory papillae, and their epicranial granulations are not as highly developed and are not as densely distributed as in other riodinids (DeVries, 1991). DeVries (1991) suggested two possible mechanisms of sound production in *Eurybia*: (1) grating epicranial granulations against the distal edge of the prothorax, or (2) producing calls in a manner similar to larvae in the butterfly family Lycaenidae, which produce a shivering in body segments when producing calls, although the actual mechanism has not been comprehensively documented.

Here, we describe the organ and mechanism of sound production in the eurybiine butterfly caterpillar *Eurybia elvina* Stichel (Riodinidae) (Fig. 1).



Fig. 1. An adult *Eurybia elvina* being eaten by a praying mantis. In the background is an inflorescence of the hostplant *Calathea latifolia*.

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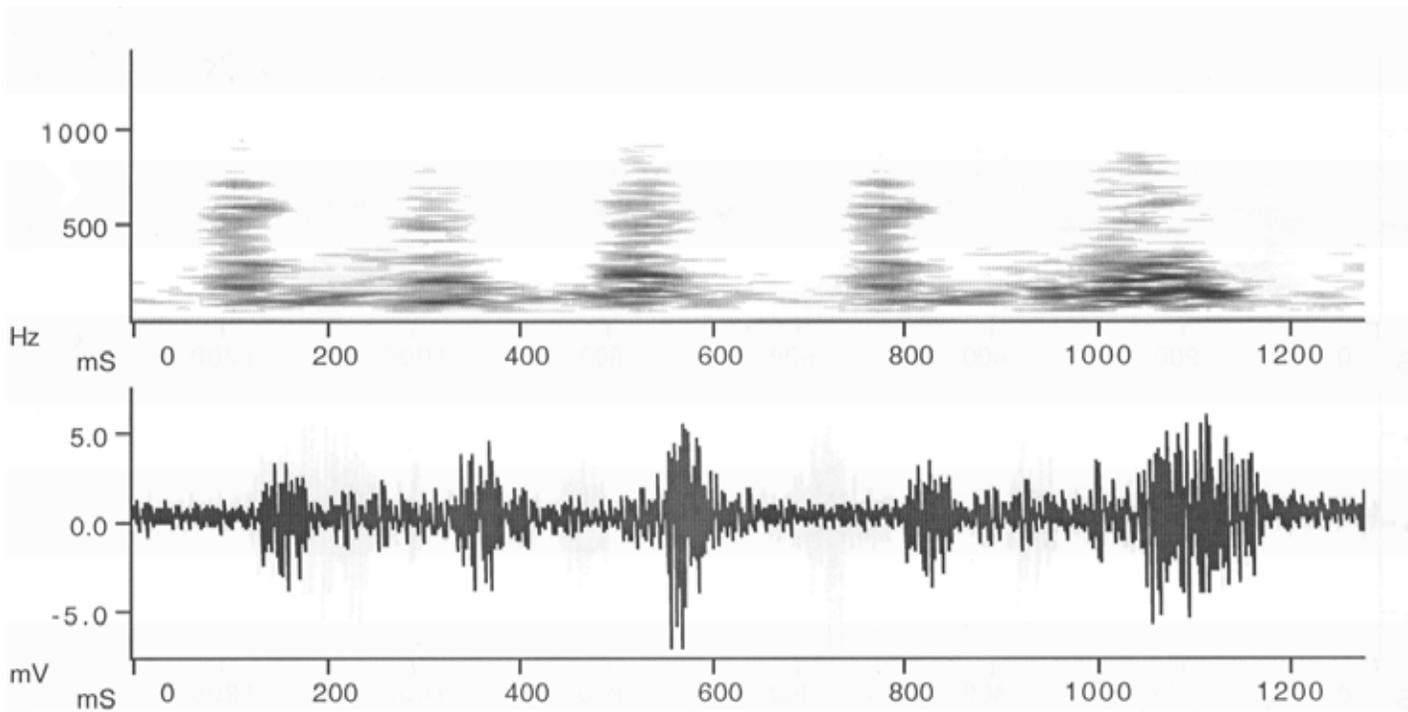


Fig. 2. Waveform (bottom) and spectrogram (top) of a pulse train produced by a *E. elvina* caterpillar.

METHODS

This research was conducted during October and November, 1997, in Gamboa and Pipeline Road, Soberania National Park, Panama, where *E. elvina* caterpillars were collected from the inflorescences of the hostplant *Calathea latifolia* (Marantaceae) along with their attendant ant, *Ectatomma ruidum* (Formicidae). Larvae were observed producing sound under a dissecting microscope. Sound production was detected with a Knowles BU-3170 and BU-1771 accelerometer taped to a plant branch. The BU-3170 has an optimal sensitivity range of 20-3000 Hz, while the BU-1771 has a range of 50-3000 Hz. Recorded vibrations were amplified with an Archer Mini-Amplifier and recorded on a Nagra IV-SJ Tape Recorder. Two late instar larvae were immersed in Quinter's solution (see DeVries, 1997) and upon inflation, were each transferred to a vial of 70 percent alcohol. After a week, they were transferred to new vials of 70 percent alcohol. The specimens were then critical point dried, affixed to stubs, and gold sputter coated before examination with a scanning electron microscope (SEM).

RESULTS

Dissecting microscope observations

E. elvina calls produced rapid trains of pulses (Fig. 2) that matched DeVries's (1991) description of calls by members of the genus *Eurybia* as trains of "eh-eh-eh-eh . . ." with 12-15 pulses produced per second. Larvae called while walking and foraging, when both alone and tended by *E. ruidum* ants. With an ant guard, larvae often began call production just before beginning to walk.

As a caterpillar called, it rapidly oscillated its head laterally.

Each oscillation temporally matched the production of a single pulse, and when the caterpillar ceased its head movements, call production also stopped. Calls were only detected when the anterior portion of the caterpillar was in contact with the substrate; when the head region was not on the substrate, i.e., when it was partially off the plant branch or when its head was lifted off the substrate, no calls were detectable.

SEM examination

With *E. elvina* inflated, the cervical membrane usually tucked within the prothorax is visible, as is the dorsum of the head (Fig. 3-4). Scattered throughout the dorsal surface of the head are hemispherical protuberances that increase in size and density further away from the medial line (Fig. 4-5) and match DeVries's (1988, 1991) description of epicranial granulations. The cervical region itself is covered with tubercles (Fig. 4) that are rounded near the medial line and become sharper laterally, resembling barbs or teeth, all less than 10 microns in length (Fig. 6). With a living, uninflated caterpillar, these cervical teeth would oppose the surface of the head. In fact, on the caterpillar's lateral surfaces, even when inflated, the teeth can be seen in opposition to the epicranial granulations on the head (Fig. 7-8).

CONCLUSIONS

A *E. elvina* larva produces substrate-borne signals by oscillating its head laterally, thereby scraping the teeth that cover the cervical membrane against the epicranial granulations found on the surface of the head. Several observations support this conclusion. Sound is produced only when the caterpillar oscillates its head, and each oscillation of the head matches the production of a single pulse of

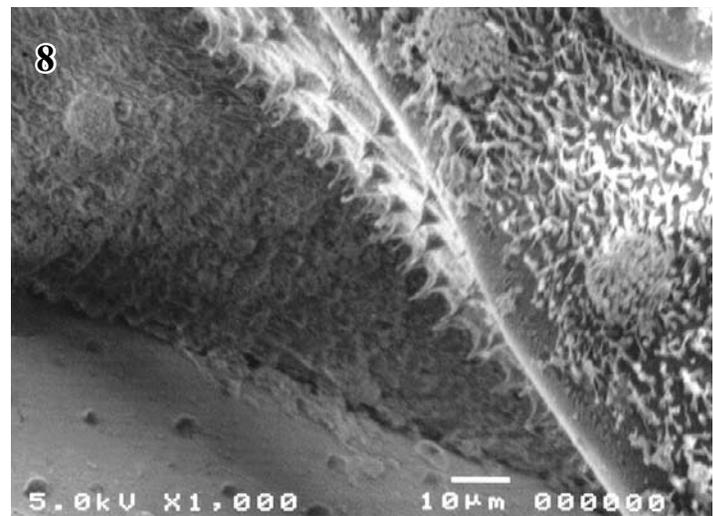
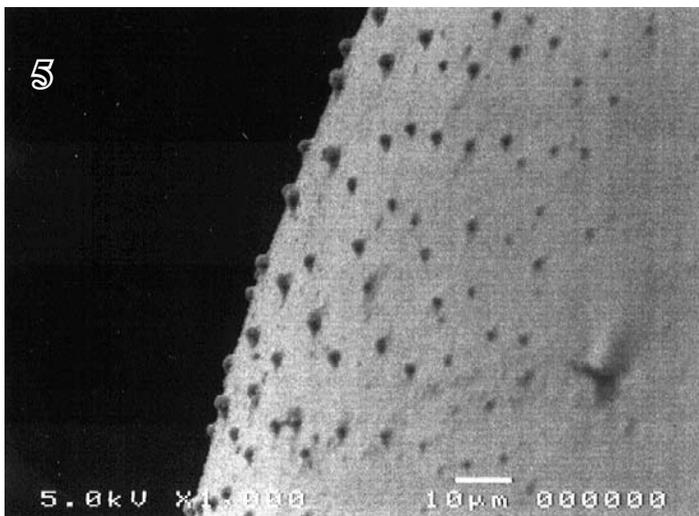
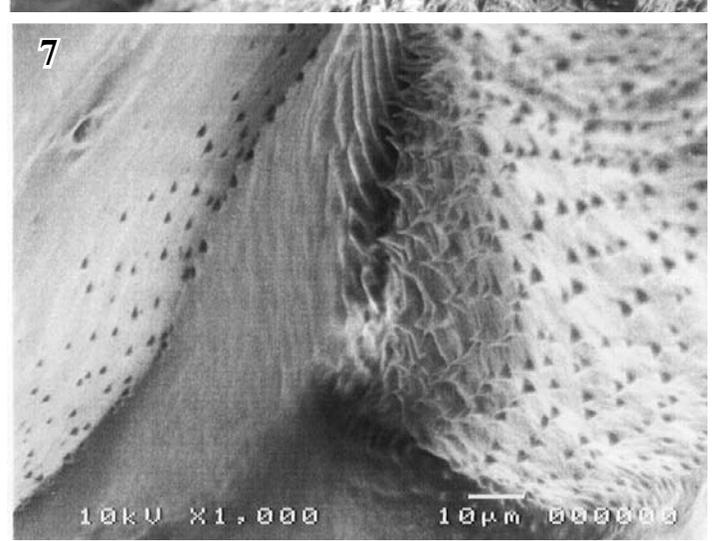
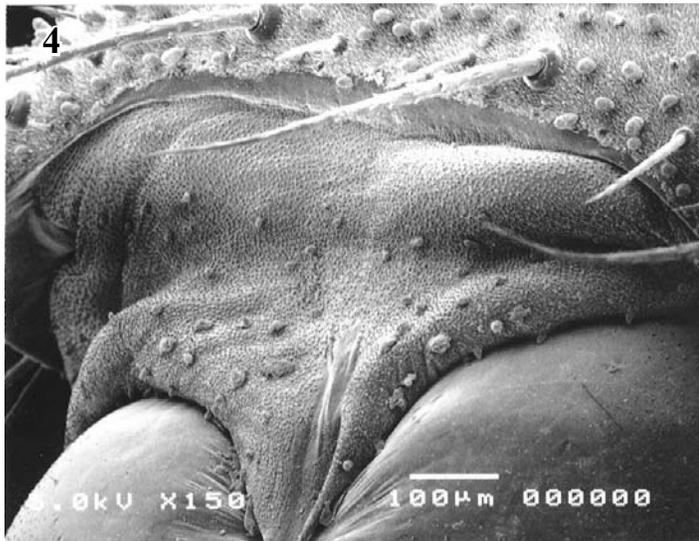
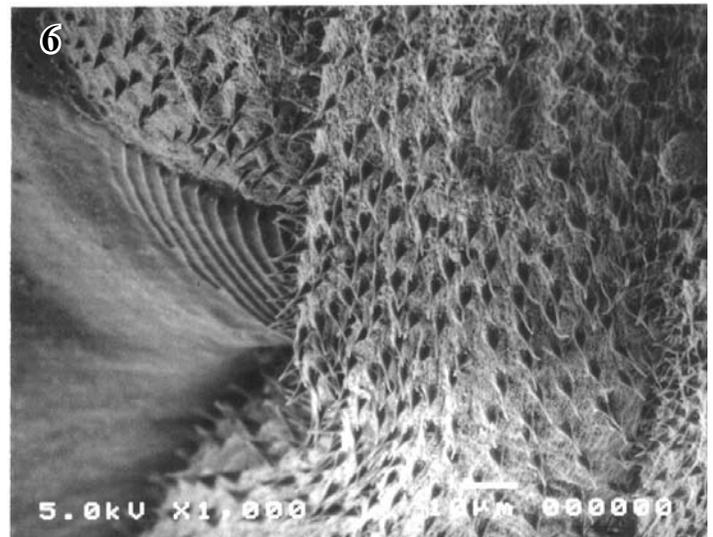
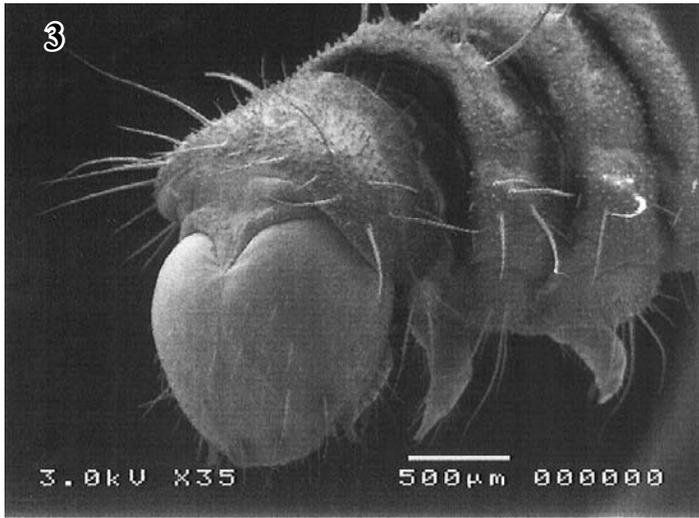


Fig. 3. Inflated *Eurybia elvina* larva with an exposed cervical membrane (scale bar = 500μm).

Fig. 4. Closeup of the cervical membrane connecting the prothorax to the head (scale bar = 100μm). Sharpened tubercles carpet the membrane's surface. Epicranial granulations are faintly visible dotting the lateral margins of the head.

Fig. 5. The larval sound-producing organ of *E. elvina*. A close-up of the margin of the dorsal surface of the head, moving laterally right to left. The lower right-hand corner of the micrograph represents the most medial portion of the head pictured. The epicranial granulations on the surface of the head occur in greater density and are larger further away from the medial line (scale bar = 10μm).

Fig. 6. Sharp teeth stud the lateral surface of the cervical membrane (scale bar = 10μm). These teeth are particularly pointed away from the medial line.

Fig. 7. Rows of teeth and epicranial granulations lie in direct opposition to each other, as seen on the lateral surfaces of the inflated *E. elvina* larva pictured here. On the lateral margins of the caterpillar, the epicranial granulations, left, oppose the sharp teeth that cover the cervical membrane, right (scale bar = 10μm).

Fig. 8. The pointed teeth of the cervical membrane lie above the hemispherical granulations on *E. elvina*'s head, bottom, as seen here on the inflated caterpillar's lateral margins (scale bar = 10μm).

sound. In addition, when a caterpillar's head is not in contact with the substrate, no sounds are detectable, matching observations of those riordinids that produce sound with vibratory papillae (DeVries 1991). DeVries (1988) has noted that when *T. irenea* calls, attendant ants pay particular attention to its head, the origin of its substrate-borne signals. Likewise, Horvitz *et al.* (1987) found that attendant ants of *E. elvina* pay special attention to the caterpillar's prothoracic shield, an observation that may be explained by the fact that the cervical membrane lies just under this shield and is the site of sound production.

E. elvina larvae produce calls in a distinct, though related manner to other riordinids, making use of epicranial granulations for sound production, as do members of the tribes Lemoniadini and Nymphidiini. Whether this particular method of call production is widespread within the Eurybiini is unknown. Larvae in the eurybiine genus *Alesa* also produce calls, but lack vibratory papillae (DeVries, 1997; DeVries and Penz, 2002); no observations on sound production in members of the genus *Mimocastnia*, the other member of the tribe, have been made.

E. elvina does not have the same sound-producing mechanism as *Arhopala madytus* (Fruhstorfer) (Hill, 1993) or *Jalmenus evagoras* (Donovan) (Travassos, 1997), the two lycaenids for which a larval organ for sound production has been described, although, like these two lycaenids, it produces sound via stridulation.

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