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A morphological search for the sound mechanism of *Hamadryas* butterflies (Lepidoptera: Nymphalidae)

Julián Monge-Najera

Museo de Zoología, Universidad de Costa Rica, Costa Rica

Francisco Hernández

Facultad de Microbiología, Universidad de Costa Rica, Costa Rica

Abstract. At least seven locations have been proposed for the sonic mechanism of *Hamadryas* butterflies, which has not been identified to date. Using light microscopy, five species of *Hamadryas* (including a "mute" population) were compared with *Siproeta stelenes, Ancirtia fatima* and *Ectima thecla,* which do not emit audible sound. Three macrostructures were found exclusively *inHamadryas:* the abdominal rami, and in the forewings, a hemispheric membrane in the costal cell and the swollen base of the subcostal vein. Only the third appears to be related to sound emission (possibly, percussion by clapping the wings). Thus, the forewings appear to be the most feasible location for the sound emission mechanism in *Hamadryas.*

Introduction

Despite Darwin's mention of the phenomenon in his books (Darwin, 1839; 1871), the loud sound emissions of *Hamadryas* —a genus of Neotropical butterflies—are not widely known by entomologists. At least seven locations of the thorax, forewings and abdomen have been proposed for the still unidentified sound mechanism, but experimentation has proven difficult (Swihart, 1967; Monge-Najera, 1991).

Considering the intensity and frequency of the sound, the structures which produce it must be relatively large (Swihart, 1967; Cromer, 1978) and possibly detectable in a study of the external gross morphology. Surprisingly, such a study had never been attempted before.

This paper compares external structure in eight ecologically related Neotropical species: I) five sound-emitting *Hamadryas* species from Costa Rica: *H. amphinome, H. feronia, H. guatemalena, H. glauconome* and *H. februa;* specimens of *H. februa* from a Venezuelan population which does not emit audible sound (Otero, 1988) were also included; II) three species which do not emit sound: a) *Siproeta stelenes,* similar to *Hamadryas* in size, territorial behavior and diet; b) *Anartia fatima,* also territorial but smaller and nectarivorous and c) *Ectima thecla,* a member of a genus that is phylogenetically and ethologically close to *Hamadryas* (Jenkins, 1985).

Methods

The insects were fixed in KAAD for at least a week and preserved in 75% ethanol. Scales and debris were eliminated with a brush and by manual or ultrasonic agitation while submerging the body (6 mm) and the wings (3 mm) in commercial bleach (approximately 2.5 % sodium hypochlorite). After a rinse in distilled water, the specimens were dried with the help of a vacuum evaporator or in air.

All illustrations are based on camera lucida drawings. To facilitate observation, some translucent parts were coated with gold as for scanning electron microscopy and observed with a light dissection microscope. Ink was added to check possible communication among veins.

A total of 97 specimens of eight species were studied, as follows: *Hamadryas februa* (5 ♀, 30 ♂), *H. feronia* (2 ♀, 5 ♂), *H. guatemalena* (1 ♀, 8 ♂),*H. glauconome* (1 ♀, 1 ♂), *H. amphinome* (1 ♀, 1 ♂), *S. ste1enes* (2 ♀, 24 ♂), *A. fatima* (3 ♀, 11 ♂) and *E. thecla* (2♂)

Results

The structure of forewings and the general thorax and abdomen plans are similar in all taxa, independent of sex (Figs. 1-9). The only outstanding characteristics are the presence of the hypandrium and rami, in male *E. thecla* and *Hamadryas* spp., respectively (Figs. 7 C, 8 A,B and 9 A,B), and three structures of the forewings: Vogel's organ, and in *Harnadryas,* the costal cell membrane and the swollen base of the subcostal vein (Figs. 2 and 7B).

The hypandrium and rami are structures associated with the male genitalia. The hypandrium has the shape of a curved lamina and the rami are a pair of rods (Figs. 7 C, 8 A, B and 9 A, B).

"Vogel's organ" (a term coined by Otero, 1988) is developed in both sexes of *Hamadryas* and less defined in the other genera. This organ (Fig. 7 B) was found in satyrids early in the century (Vogel, 1912) and occupies the base of the Cu vein. It has a rigid cap mounted on a flexible ring. There are four chambers under the cap; ink added to them does not reach the adjoining veins, suggesting a lack of direct connection.

The costal cell membrane (present in *Hamadryas* only) has the shape of an elongated coppola and is located in the wing base (Fig. 7 B). This membrane, which is inflated in the living insect, can be easily ruptured (and thus deinflated) during manipulation of the specimen. In *Hamadryas,* the strong subcostal vein is highly "swollen" and reaches a diameter about 2-3 times that of the equivalent vein of silent species.

All *Hamadryas* have three structures that are lacking in the species which do not emit sound: a) in the abdomen, the rami and b) in the forewings, the costal cell membrane and the swollen base of the subcostal vein.

Discussion

To evaluate the plausibility of the role of each structure in sonic emission, it is useful to consider how sound is produced by organisms.

There are three basic mechanisms, all known in the Lepidoptera (MongeNájera and Morera, 1987): vibration of a filament, vibration of a membrane and percussion.

None of the structures found appears capable of vibrating as a filament. The costal cell membrane and Vogel's organ could act as a vibrating membrane but they lack the necessary muscle and the second also occurs in "silent" species (Figs. 1 and 2). Swihart (1967) experimentally showed the auditory function of the costal cell membrane; the function of Vogel's organ, proposed to be a hearing organ by Vogel himself (1912), has not been tested (it may be specialized for detecting predatory bats, as suggested by its rigidity and smaller size; see Cromer, 1978).

Percussion could be carried out by any mobile structure hitting against another; this includes the antennae and legs (both never suggested as sound organs in the literature on *Hamad ryas)* and the rami and wings. The antennae appear too soft for loud percussion and the legs do not participate, since -very infrequently- perching individuals produce sound while the legs are motionless (but they clap the wings as they emit sound during perching; JMN, personal observation). The rami do not show articulations (Jenkins, 1983) and are more probably structures used by females "to evaluate the male" during copulation attempts, as suggested in general for complex, rigid sexual structures by Eberhard (1985). The same applies to the hypandrium of the mute *Ectima.*

In contrast with the ether structures, the swollen base of the subcostal vein in the forewings (exclusively present in species that emit sound) could be a reinforcement for percussion. A strong venation may allow sound production when the insect claps its wings (less probably, sound may result from chitin flexing or snapping during a modified wing beat). Interestingly, the "mute" Venezuelan *Hamadryas* do not present any defined morphological difference from sound emitting Hamadryas. Their silence may be an ethological rather than a morphological characteristic.

In conclusion, the forewings are the most feasible location for the sound emission mechanism in *Hamadryas* , possibly in relation to clapping, but the exact nature of the mechanism remains to be identified.

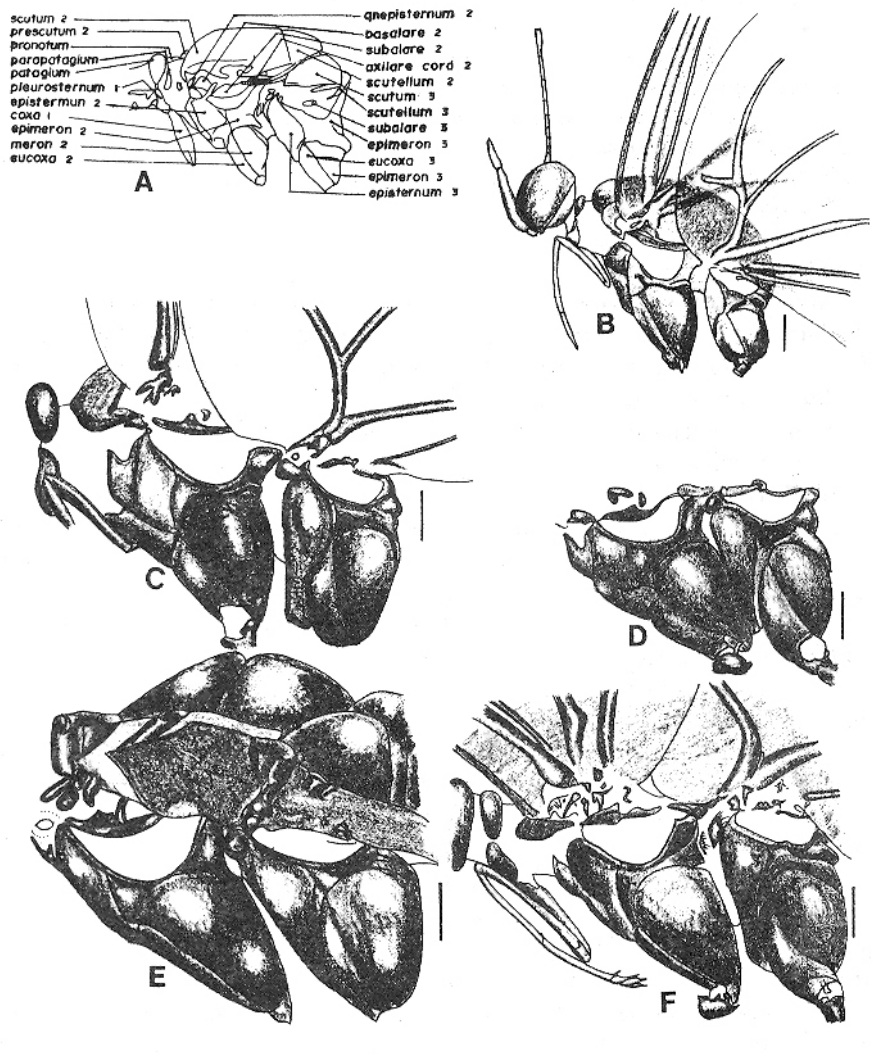

Fig. 1. Lateral view of thorax. A. Nomenclature (from Scott, 1985). B. Male *F. thecla.* C. Male *E. fatima.* D. Female *E. fatima* (wings removed). F. Male S. *stelenes.* F. Female S. *stelenes.* Bars 1 mm.

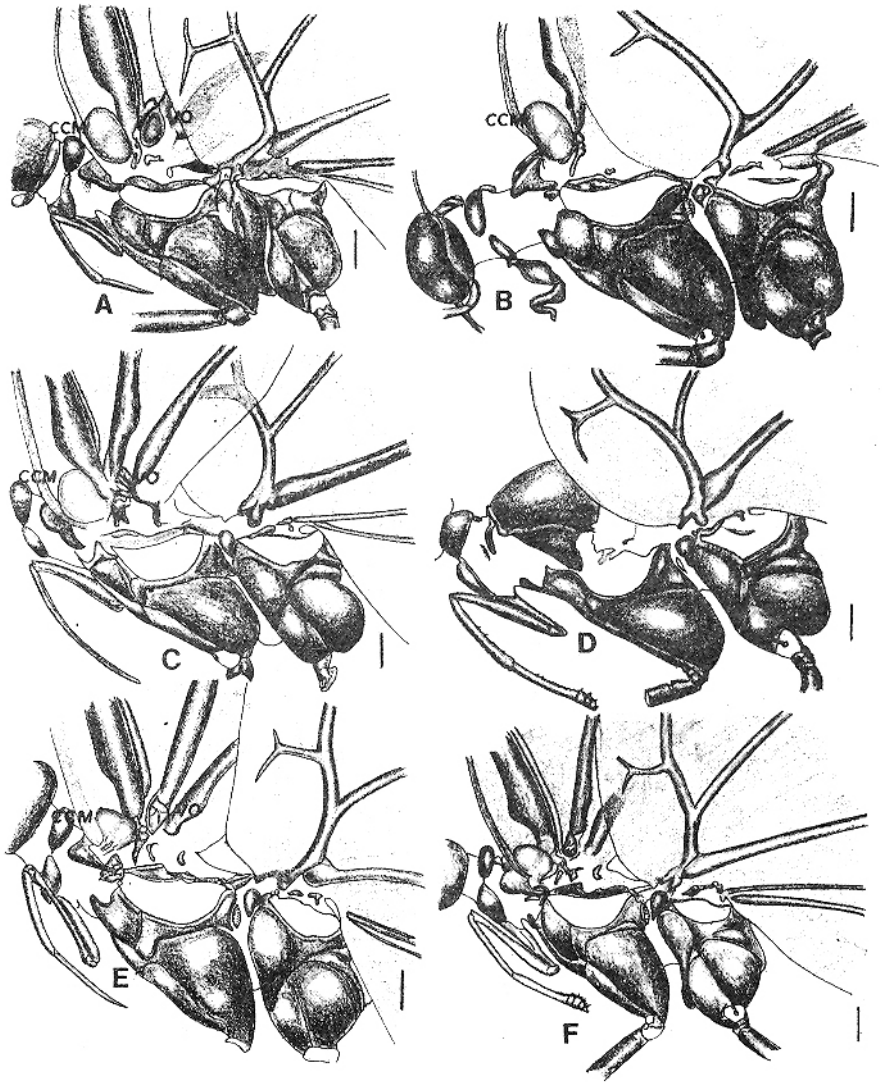

Fig. 2. Lateral view of thorax. A. Male *H. februa.* B. Female *H. februa.* C. Male *H. feronia.* D. Female *H. feronia.* E. Male *H. guatemalena.* F. Female *H. guatemalena.* Bars 1 mm.

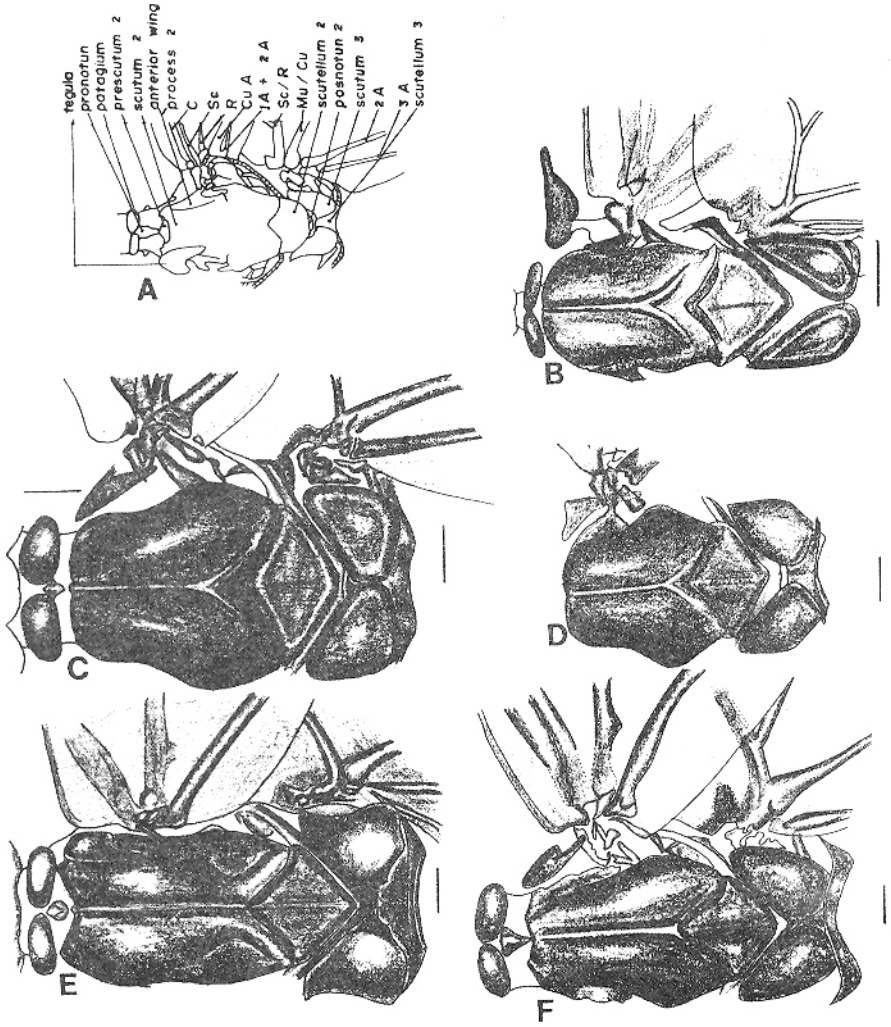

Fig. 3. Dorsal view of thorax. A. Nomenclature (from Scott, 1985). B. Male *E. thecla.* C. Male *E. fatima.* D. Female *E. fatima* (wings removed). E. Male S. *stelenes.* F. Female S. *stelenes.* Bars 1 mm.

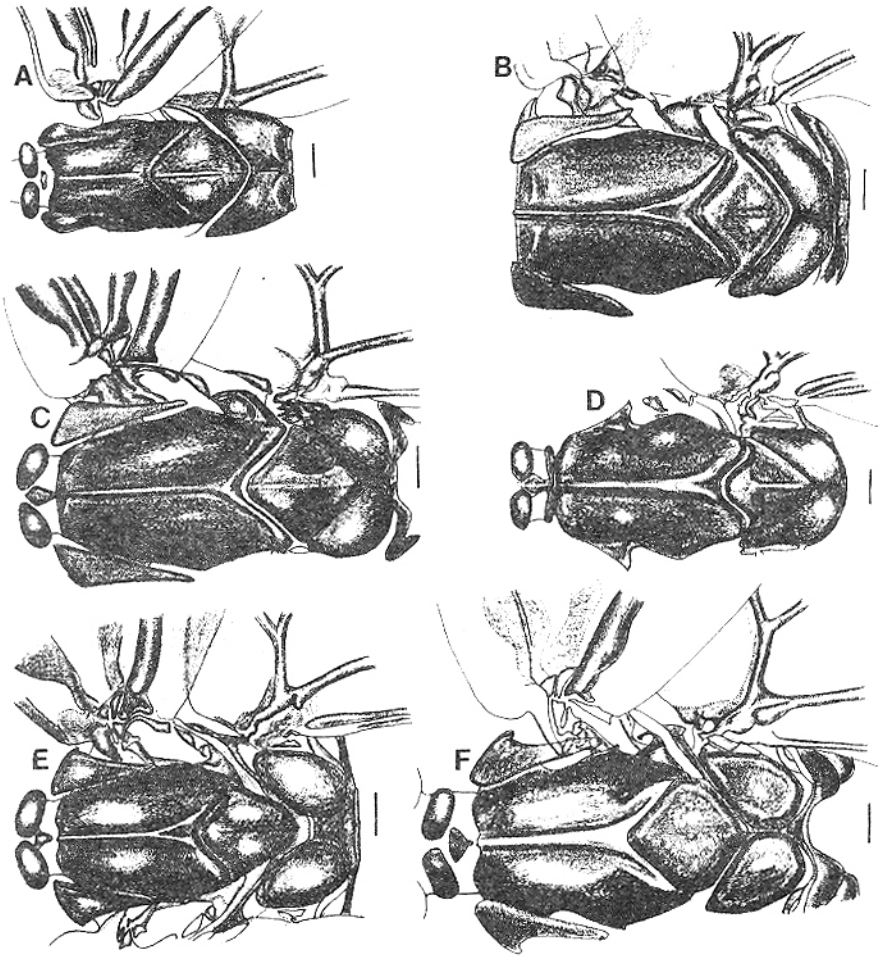

Fig. 4. Dorsal view of thorax. A. Male *H. februa.* B. Female *H. februa.* C. Male *H. feronia.* D. Female *H. feronia.* E. Male *H. guafemalena.* F. Female *H. guatemalena.* Bars 1 mm.

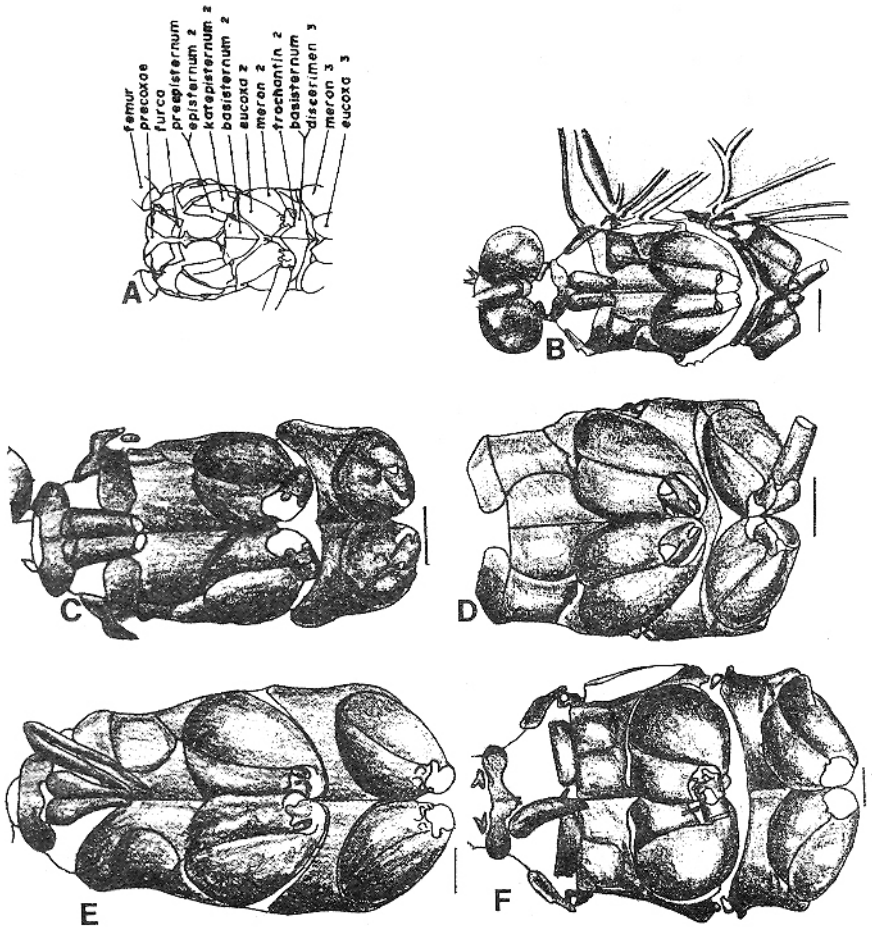

Fig. 5. Ventral view of thorax. A. Nomenclature (from Scott, 1985). B. Male *E. thecla.* C. Male *E. fatima.* D. Female *F. fatima* (wings removed). E. Male S. *stelenes.* F. Female S. *stelenes.* Bars 1 mm.

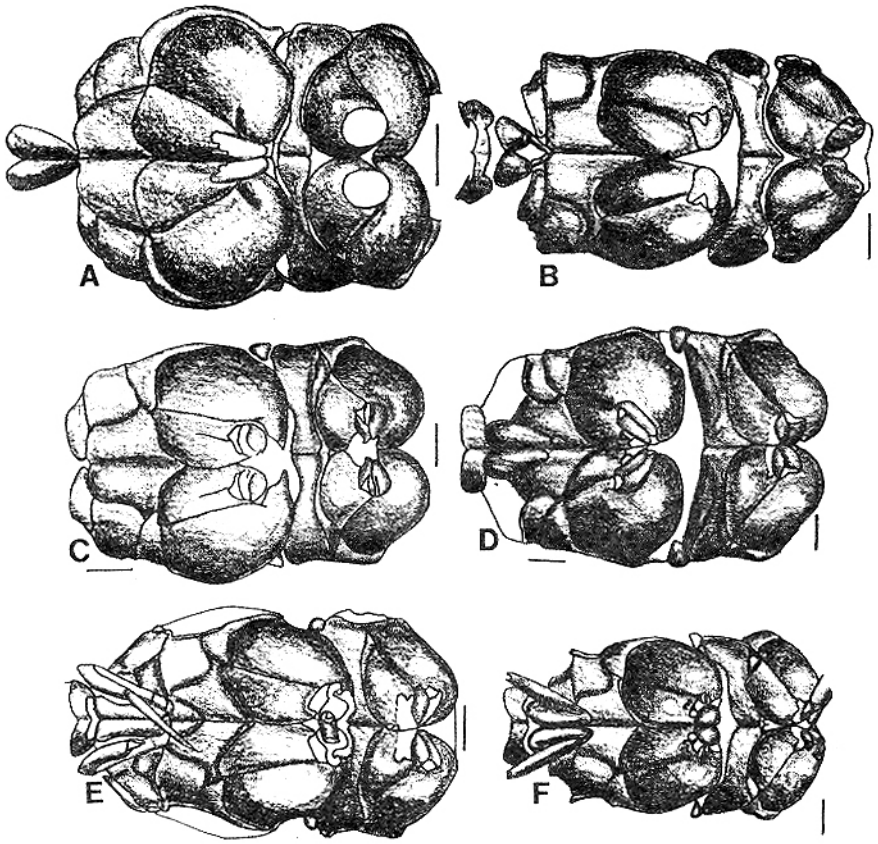

Fig. 6. Ventral view of thorax. A. Male *H. februa.* B. Female *H. tebrua.* C. Male *H. feronia.* D. Female *H. feronia.* E. Male *H. guatemalena.* F. Female *H. guatemalena.* Bars 1 mm.

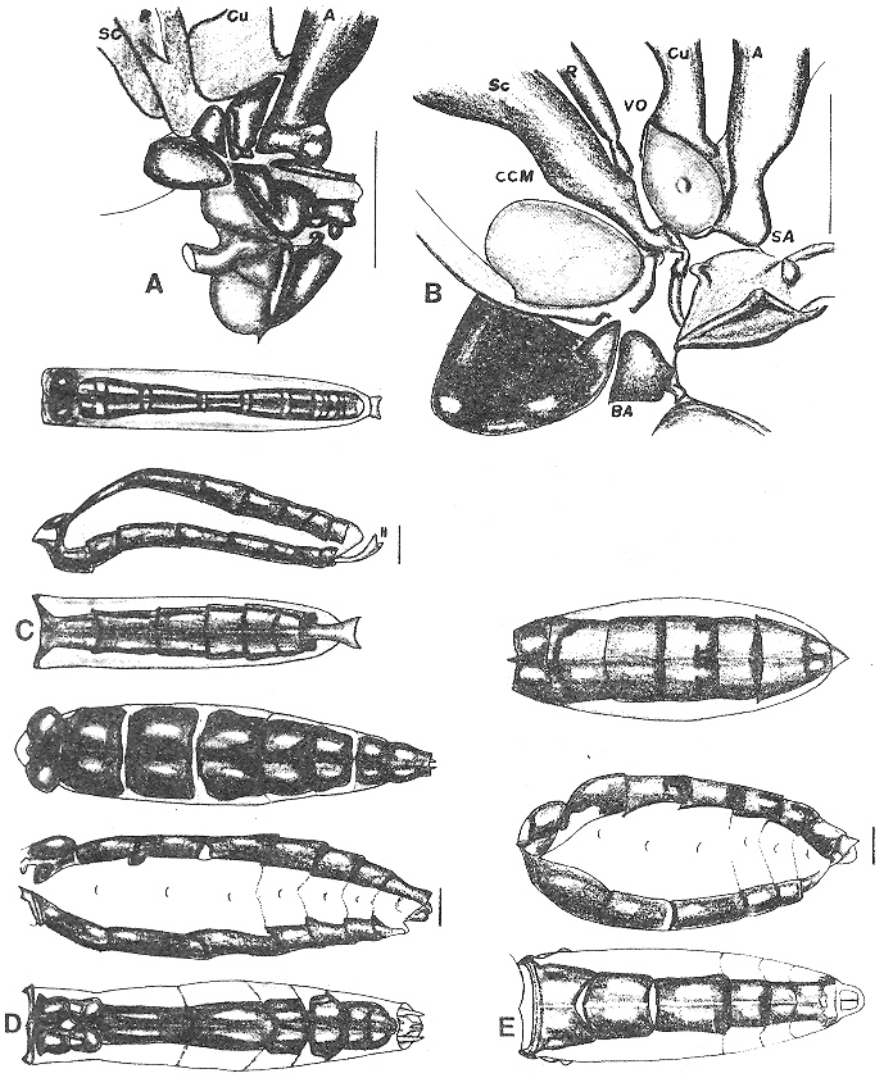

Fig. 7. Dorsal (A) and ventral (B) sides of the forewing base of male *H. februa.* Veins: Sc subcostal, R radial, Cu cubital, A anal. Other structures: BA basalare, H hypandrium, MCC membrane of costal cell, SA subalare, VO Vogel's Organ. From above: dorsal, lateral and ventral view of abdomen in male *E. thecla* (C), and *A. fatima* (D: male, E: female). Bars 1 mm.

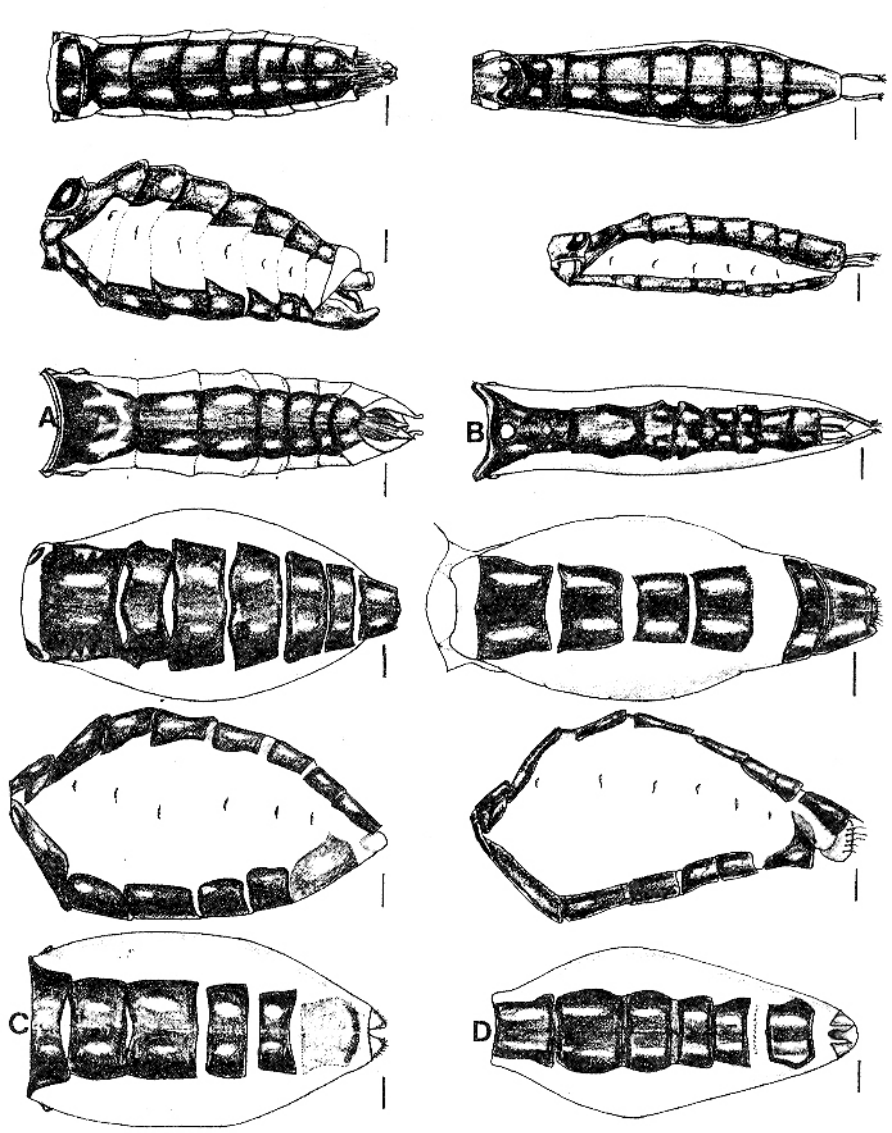

Fig. 8. From above: dorsal, lateral and ventral view of abdomen in: A. Male S. *stelenes.* B. Male *H. februa.* C. Female S. *stelenes.* D. Female *H. februa.* Bars 1 mm.

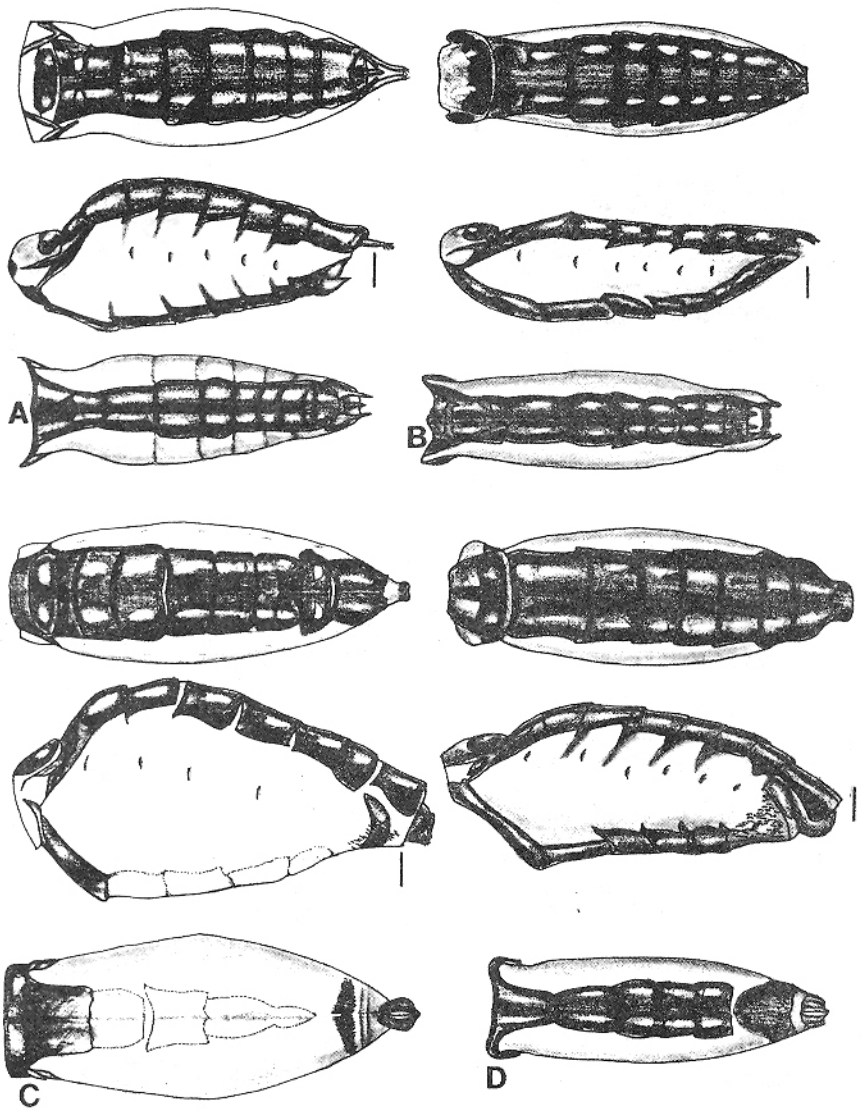

Fig. 9. From above, dorsa, lateral and ventral view of abdomen in: A. Male *H. ferania.* B. Male *H. guatemalena.* C. Female *H. feronia.* 0. Female *H. guatemalena.* Bars 1 mm.

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