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EARLY STAGES OF THE ENTOMOPHAGOUS METALMARK BUTTERFLY *ALESA AMESIS* (RIODINIDAE: EURYBIINI)

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ABSTRACT. The immature stages of *Alesa amesis* are described in detail for the first time, and then compared to those of its sister genus, *Eurybia*.

Additional key words: *Eurybia*, morphology, myrmecophily, caterpillar calls.

The riodinid butterfly *Alesa amesis* (Cramer, 1777) is a widespread and often locally common member of the tribe Eurybiini with a geographic range that includes Brazil, the Guyanas, Venezuela Colombia, Ecuador, and Peru. Recently we showed that *A. amesis* has an obligate association with *Camponotus femoratus* (Fabricius, 1804) ants, and that the entomophagous caterpillars possess morphological and behavioral adaptations for feeding on Homoptera prey. These biological aspects are summarized briefly as follows. At one site in Amazonian Ecuador we found that female *A. amesis* oviposited only in the presence of *C. femoratus* ants tending aggregations of several genera of Membracidae or Atelionidae (Homoptera) that fed on six families of plants. Oviposition by *A. amesis* occurred either adjacent to aggregations of Homoptera, or directly on an individual nymph. Available evidence suggests that *A. amesis* caterpillars feed entirely on Homoptera nymphs, and that compared to other herbivorous relatives, there has been an evolution of leg-length to accommodate their entomophagous diet. Greater comparative, behavioral, morphometric and analytical details are provided in DeVries and Penz (2000).

Given that there is little detailed information on early stages of most species of Eurybiini, and on *Alesa* in particular, here we present a detailed description of *Alesa amesis* early stages and compare them to species of their sister genus, *Eurybia* (Harvey 1987, Hanner 1998).

Materials and Methods

Field work was conducted at the La Selva Lodge, Garza Cocha, Sucumbios Province, eastern Ecuador in the upper Amazon Basin, 75 km E.S.E. of Coca (0°29′50.3″S; 76°22′28.9″W). A detailed site description is provided in DeVries and Walla (2001).

Early stage material of *A. amesis* was field-collected (caterpillars were first placed in Quinter's solution, see protocol in DeVries 1997), then stored in 70% alcohol, and later examined using light microscopy. Except for the second instar, we examined all *A. amesis* early stages. Descriptions of caterpillar morphology follow the terminology of Peterson (1962), Cottrell (1984) and Stehr (1987). Preserved material of four *Eurybia* species was compared to first and fifth instar caterpillars, and pupae of *A. amesis*. This material included: fifth instar caterpillars of *A. amesis*, *Eurybia patrona* Weymer, 1874, *E. elvina* Stichel, 1910, *E.* nr. *nicaeus* (Fabricius, 1775) and *E. lycisca* (Westwood, 1851), and pupae of *E. lycisca*. Comparative differences and the sources of information are presented in Table 1, and Figs. 5–17. Comparative voucher material of *Alesa* and *Eurybia* are in the Museo Nacional de Ecuador and the collection of DeVries.

Results

Egg. (Fig. 1) (n = 2) Measurements: 0.83 mm wide, 0.4 mm tall. White upon being laid, turning pale green within 24 hours; base broad, tapering gently towards apex; chorion heavily adorned with rounded sculpturing that is interconnected with numerous small tubercles. Egg bears little resemblance to lozenge-shaped eggs of the sister genus *Eurybia*, but it is reminiscent of the more distantly related *Synargis* (see illustrations in DeVries 1997).

First instar. (Fig. 4) (n = 2) Head pale yellow-brown with short white plumose setae on anterior portions of epicranium and frons. Body white with short, white, finely barbed setae arising from brown pinnacula; dorsal pores on T1 and A1–A8; lateral body wall extended, flange-like, contacting substrate and concealing ventral side of body. Prothoracic shield pale yellow-brown, somewhat produced anteriorly and partially covering head; anterior margin of prothroacic shield with white, barbed, forward-projecting setae. Segments T1–T3 with distinct, pale brown dorsolateral crescent-shaped marks; thoracic legs white and distinctly elongate. Prolegs white. Anal plate pale brown,

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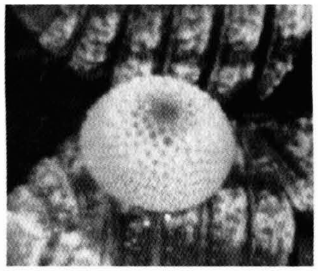

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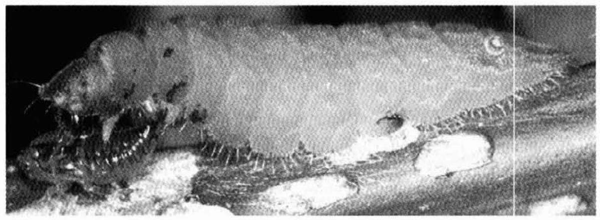

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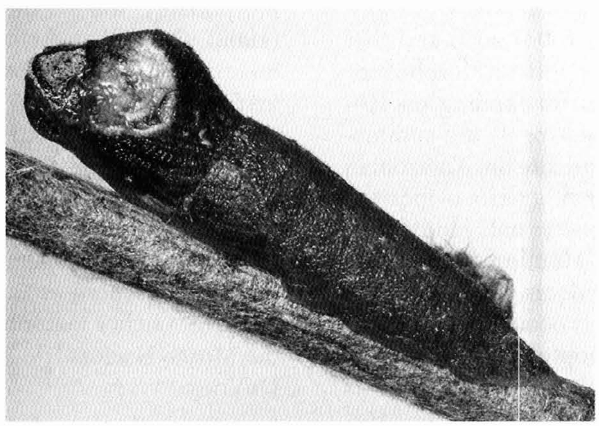

FIGS. 1–3. *Alesa amesis* early stages in nature. **1,** Egg deposited directly on the abdomen of a membracid nymph. The overall form differs dramatically from the egg of *Eurybia* (illustrated in DeVries 1997:5). **2,** Fifth instar caterpillar using thoracic legs to grasp its membracid prey. Note shortening of body segments to expose thoracic legs. **3,** Pupa. Head oriented to the left.

narrower than remaining body segments. No evidence for tentacle nectary organs or call production found in this instar.

Second instar. No specimens of this instar were found.

Third instar. (n = 3) Similar to fifth instar, and possessing bulb-shaped cuticular spinules covering body. As is general myrmecophilous riodinids (summarized in DeVries 1997), all third and subsequent instar caterpillars possessed a pair of tentacle nectary organs (hereafter TNOs) on segment A–8 (Figs. 2, 5, 6, 8). As in other riodinid species the TNOs of *A. amesis* produced secretions only when solicited by attending ants (DeVries & Penz 2000). The ability to produce calls was also functional in this and all subsequent instars.

Fourth instar. (n = 6) Except for being smaller, indistinguishable from fifth instar. Premolt duration from fourth to fifth instar 36 to 48 h.

Fifth instar. (Figs. 2, 5–11) (n = 9) **Head:** black, anterior portion of epicranium and frons with minute tubercules and long simple setae; short simple setae distributed along entire surface of head; labrum narrow, exposing base of mandibles. **Body:** uniformly green except for light brown prothoracic shield and openings of tentacle nectary organs on A8 (some fifth instars turned brown a few days after molting, and lost all traces of green). Lateral body wall extended, flange-like and with plumose setae, contacting substrate from A2–A9 and concealing prolegs and ventral side of body (Fig. 2); ventrolateral segmental areas reduced in T1–T3 and A1, thoracic legs visible in lateral view (Fig. 2, see also DeVries & Penz 2000). **Cuticle:** covered with short spines set on broad, sclerotized bases armored with 4–8 short points (most commonly with 6 points). **Prothoracic shield:** produced anteriorly and covering head; in dorsal view, anterior margin of prothoracic shield with a distinct medial excavation and 3 pairs of long plumose setae. **Thoracic legs:** white,

TABLE 1. Comparative morphology of the early stages of *Alesa amesis* and *Eurybia*. All comparisons were done directly from preserved material unless indicated otherwise. Supplemental sources and notes are as follows: [1] Horvitz et al. (1987); [2] Malicky (1970) discusses thickened integument in larval Lycaenidae; [3] mandible examined in detail only in *Eurybia lycisca*; [4] DeVries (pers. obs); [5] DeVries and Penz (2000). Letters in first column correspond to details in Figs. 4–17, except for "body integument" (c), and "plantae" (m).

First Instar—Fig. 4	***Alesa amesis***	***Eurybia elvina*** [1]
a. Prothoracic shield in dorsal view	longer and wider than head slightly covering head	narrower and shorter than head not covering head
b. Primary setae	numerous, short, thick and finely barbed	sparse, long and thin
c. Dorsal pores	present on prothorax and A1–A8	absent
d. TNOs	absent	present
Fifth Instar—Figs. 5–17	***Alesa amesis***	***Eurybia patrona, E. elvina, E. lycisca, E. nicea***
a. Body shape in lateral view	distinctly humped at mid-length	not humped at mid-length
b. Ventrolateral areas of body segments	T1–T3 and A1 conspicuously short, exposing legs; A2–A8 elongated and hiding prolegs	largely uniform length across all body segments
c. Body integument [2]	thicker than *Eurybia* and most other myrmecophilous riodinids	similar in thickness to most other myrmecophilous riodinids
d. Cuticular spines	long, set on sclerotized base armored with 4–8 points (most commonly 6)	short, without sclerotized base
e. Frontal and adfrontal regions of head	densely covered with thick, nub-like setae	*Eurybia patrona, E. niceaus, E. lycisca* lack these setae; *E. elvina* with some scattered, slightly thicker setae
f. Distal segment of antenna	long	short
g. Maxilla	comparatively small	comparatively large
h. Mandible	stout, with short teeth	slender, somewhat paddle-shaped, with long teeth [3]
i. Stemmata	comparatively large	comparatively small
j. Prothorax in dorsal view	covering head	not covering head
k. Thoracic legs [5]	allometrically longer than other riodinid caterpillars	not differing allometrically from other riodinid caterpillars
l. Position of spiracles on A1	centered and slightly above the spiracular line	near anterior margin and below the spiracular line
m. Plantae	comparatively broad	comparatively narrow
n. Lateroseries of crochets	crochets short and widely spaced	crochets long and densely packed
o. TNOs	externally stalked and armored	externally an un-stalked slit
p. Anal plate	small and approximately rectangular posterior margin of A8 projected to enclose anal plate	large and oval, posterior margin of A8 not projected
Pupa—Fig. 3	***Alesa amesis***	***Eurybia elvina*** [1]**, *E. lycisca***
a. Body shape	stout	slender
b. Proboscis	short	elongate, extending beyond cremaster
c. Pupation site	uncovered pupae attached to plant stems	typically concealed within sheathing stems of host plant [1, 4]

slightly darker at tarsi. Plantae of prolegs broad. **Anal plate:** rectangular, small, not well differentiated from rest of abdomen, and enclosed by posterolateral expansions of A8.

Pupa. (Fig. 3) (n = 7) Light to dark brown, elongate, tallest and widest anteriorly and tapering gradually from head to cremaster. In ventral view, antennae terminate at posterior margin of A6, and proboscis terminates distally at posterior margin of T3 (for comparison, see Horvitz et al. 1987:517 fig. 4B, DeVries 1997:137 fig. 40A). In lateral view, head and anterior portion of thorax resemble a miniature monkey face. T1 yellowish brown with an excavated anterior margin and covering head in dorsal view; thoracic spiracle red. T2–T3 with large white to green crescent mark. Pupa with skirt on A4–A10 that projects ventrally and flares over substrate; ventral side concave from T3 (approximately) to A10 to adjust for shape of pupation substrate. Silk girdle across A1; A1 and A8 conspicuously shorter than A2–A7; A9 reduced. Cremaster broad, longer than other abdominal segments, and slightly curved ventrally. Duration of pupa 15–17 days (n = 3; 2 males, 1 female). Pupation in nature occurred on small stems at base of plants associated with *Camponotus femoratus* colonies, and pupae were attended by ants.

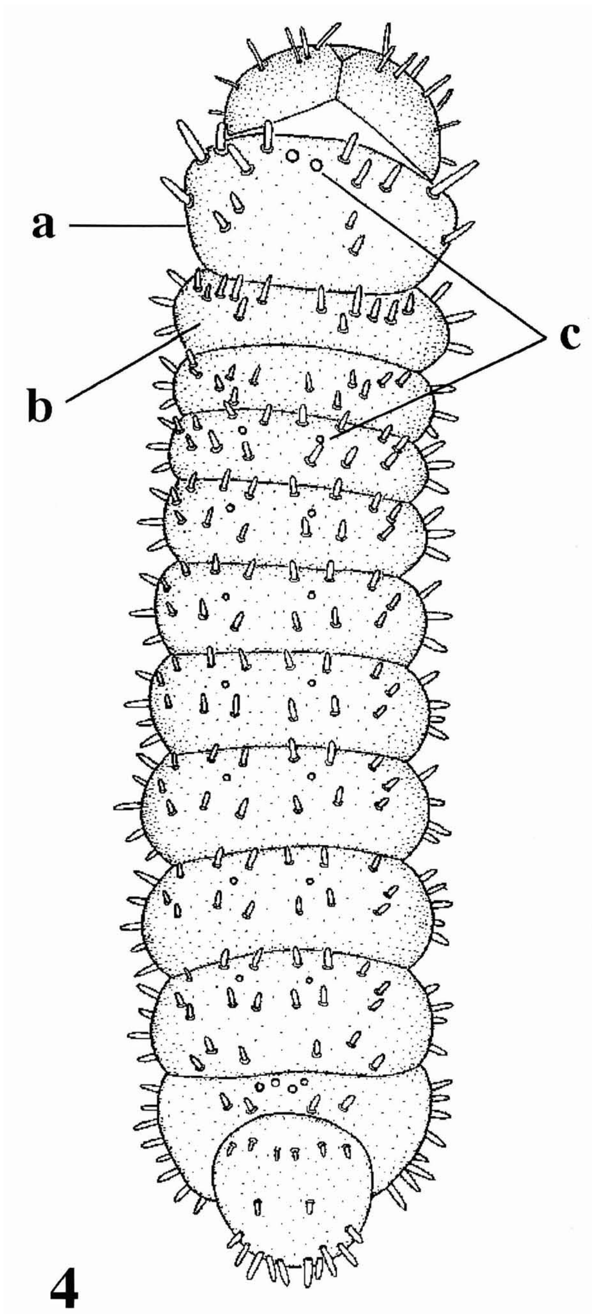

FIG. 4. First instar of *Alesa amesis*. Note size of prothoracic shield (**a**), primary setae (**b**), and dorsal pores (**c**).

DISCUSSION

Previously the only available detailed description of Eurybiini early stage morphology was that of *Eurybia elvina* by Horvitz et al. (1987). The present study shows that caterpillars and pupae of *A. amesis* may differ considerably from *Eurybia* (Table 1, Figs. 4–17). For example, although all instars of *Eurybia elvina* apparently possess TNOs (Horvitz et al. 1987) these organs are absent in first instar *A. amesis*. Other differences among *A. amesis* and *Eurybia* caterpillars include body shape, cuticular spines, relative thoracic and abdominal leg size, crochets, stemmata, antennae, and maxilla (Figs. 5–17). Traits like elongated thoracic legs, broad proleg plantae and the ventrolateral shortening of segments T1–3 and A1 in *A. amesis* caterpillars may reflect their entomophagous habit since they potentially facilitate curling of the body during prey capture and feeding. Other characteristics of *A. amesis* caterpillars may be due to their forming symbioses with ants (e.g., long cuticular spines in sclerotized, armored bases; thickened body integument; armored, stalked TNOs). However, the evolutionary basis and adaptive nature of such traits remain uncertain.

Elsewhere we have described the substrate-borne calls of *A. amesis* caterpillars, noting that the mechanism for call production within the Eurybiini was unknown (DeVries & Penz 2000). Recently Travassos et al. (in press) presented evidence suggesting that *Eurybia elvina* produce a substrate-borne call by grating cervical membrane "teeth" against hemispherical protuberances on the surface of the head. Our examination of *A. amesis* caterpillars with optical microscopy revealed a cervical membrane similar to that described by Travassos et al. (in press) for *E. elvina*—the membrane is armored with "teeth" and bears small setae and rounded protuberances. Moreover, we note the presence of rounded sclerotized areas in the dorsolateral portion of the cervical membrane in *A. amesis* and *E. lycisca, E. patrona, E. lycisca, E.* nr. *nicaeus* and *E. elvina* (indicated by arrows in Fig. 10). The function of these rounded sclerotized areas is unclear, but their potential role in caterpillar call production warrants further investigation because they occur in proximity to where epicranial granulations are well developed.

Although brief in scope, we hope this study will stimulate comparative life history work on other species of Eurybiini to further our understanding of the biology and evolution of this unusual group of riodinids.

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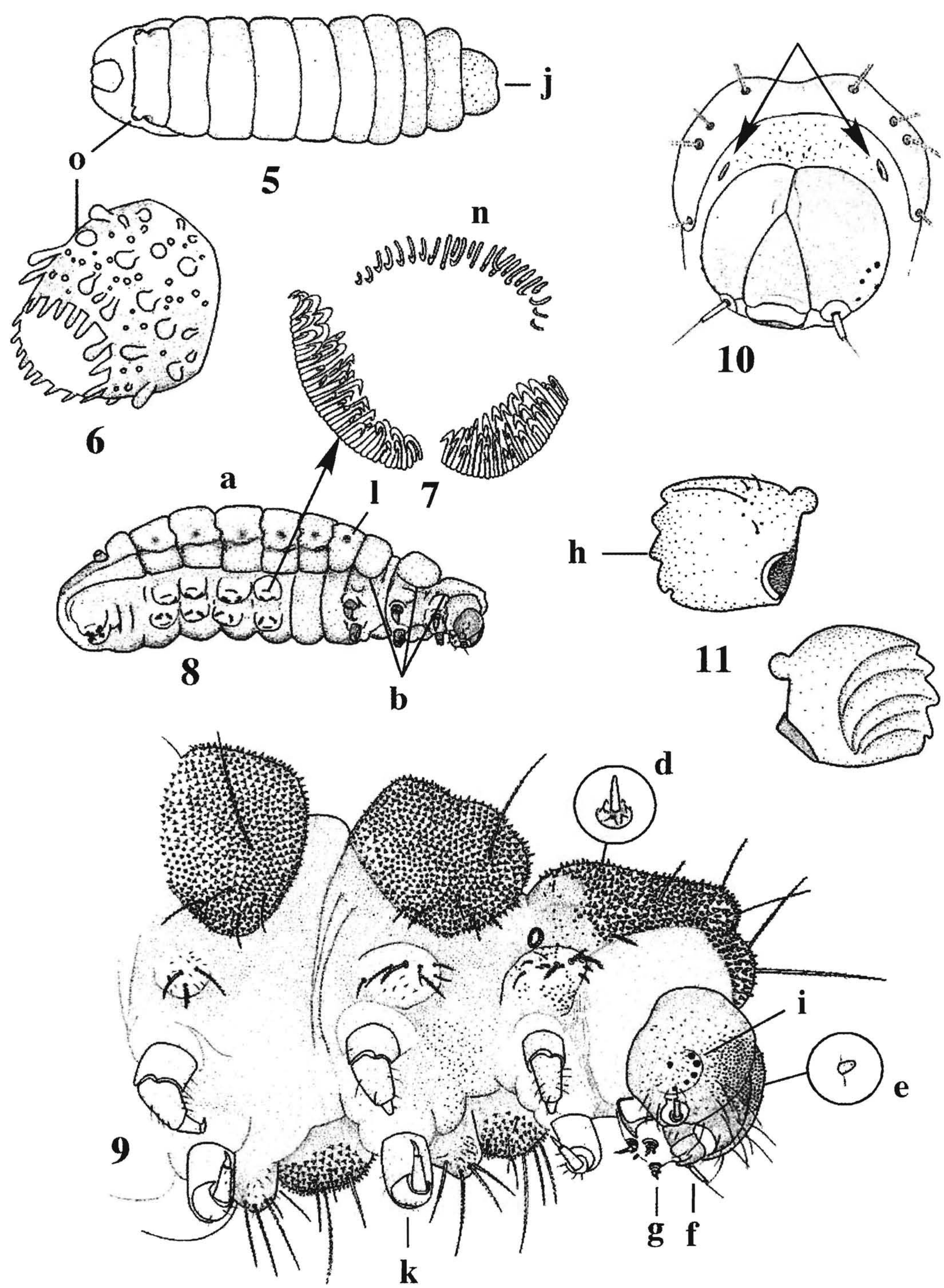
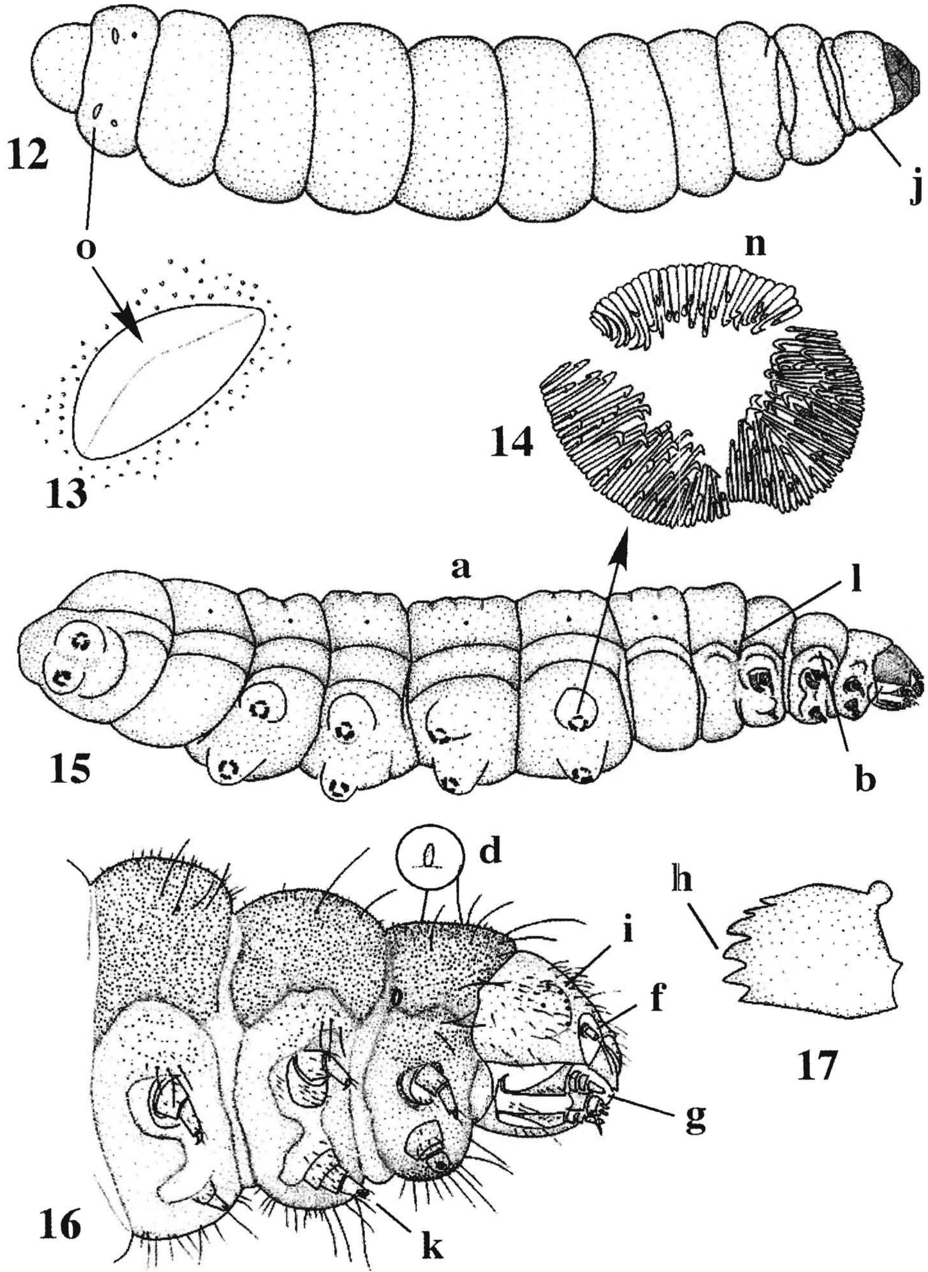


FIGS. 5–11. Details of *Alesa amesis* fifth instar caterpillar. Figs. 5–10 represent the same individual; Fig. 11 dissected from a cast skin. Letters correspond to traits listed in Table 1. **5,** Dorsal view of caterpillar, head oriented to the right. **6,** Tentacle nectary organ. **7,** Crochets of third abdominal proleg. **8,** Caterpillar in ventrolateral view. **9,** Detail of the caterpillar thorax in ventrolateral view, insets show body and head spines. **10,** Detail of caterpillar head and cervical membrane (head setae and body spines omitted), arrows indicate the round sclerotizations present on the cervical membrane. **11,** Outer (top) and inner (bottom) views of left mandible. Letters correspond to details in Table 1, except for "body integument", and "plantae".



FIGS. 12–17. Details of *Eurybia patrona* and *E. lycisca* fifth instar caterpillars. Figs. 12–16 represent the same individual *E. patrona* (Barro Colorado Island, Panama); Fig. 17, *E. lycisca* mandible drawn from a cast skin (Parque Nacional Corcovado, Costa Rica). **12,** Dorsal view of caterpillar, head oriented to the right. **13,** Tentacle nectary organ. **14,** Crochets of third abdominal proleg. **15,** Caterpillar in ventrolateral view. **16,** Detail of the caterpillar thorax in ventrolateral view, inset shows a body spine. **17,** Outer view of *E. lycisca* left mandible. Letters correspond to details in Table 1, except for "body integument", and "plantae".

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