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LARVAL MORPHOLOGY AND BEHAVIOR OF *ANTIRRHEA WEYMERI* SALAZAR, CONSTANTINO & LÓPEZ, 1998 (NYMPHALIDAE: MORPHINAE) IN COLOMBIA

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ABSTRACT. The immature stages of *Antirrhea weymeri* Salazar, Constantino & López, 1998 are described from the eastern slopes of the Cordillera Occidental (2000 m), Departamento del Valle del Cauca, Colombia. At emergence, females have around 100 oocytes, eight of which are mature eggs and another 16 are ready to receive the chorion. They lay their eggs in groups of 5–8 on the under surface of the pinnae of *Prestoea acuminata* (Arecaceae). The larvae are gregarious, and their behavior appears to be very close to that of *Morpho sulkowskyi* Kollar as far as the use of cervical and grooming glands is concerned. These new observations provide further support to a close phylogenetic relationship between *Morpho* and *Antirrhea*, as proposed by DeVries et al. (1985) and DeVries (1987).

RESUMEN. Se describen los estados inmaduros de *Antirrhea weymeri* en la vertiente oriental de la Cordillera Occidental (2000 m), Departamento del Valle del Cauca, Colombia. Las hembras recién emergidas tienen cerca de 100 oocitos, de los cuales ocho son maduros y 16 más están listos para recibir el corion. Ponen sus huevos en grupos de 5–8 en el envés de las pinnas de *Prestoea acuminata* (Arecaceae). Las larvas son gregarias y exhiben un comportamiento muy similar a las de *Morpho sulkowskyi* Kollar en relación con el empleo de las glándulas cervical y de acicalamiento. Estas nuevas observaciones corroboran la estrecha relación filogenética entre *Morpho* y *Antirrhea*, propuesta por DeVries et al. (1985) y DeVries (1987).

Additional key words: fecundity, glands, life cycle, *Prestoea acuminata*, pupal dimorphism.

Antirrhea weymeri Salazar, Constantino & López, 1998, is a local and infrequent morphinae of the Cordillera Occidental of Colombia between 1600 and 2200 m (Salazar et al. 1998, pers. obs.). Active at dusk, it remains motionless during the day and is only detected when, being disturbed, it abandons its resting place to fly low through the forest until it finds a new perch. We have always observed it in areas bordering a stream, either perched low on a shrub or on rotting trunks on the forest floor. *Antirrhea weymeri* is illustrated in D'Abrera (1984:368) as *Antirrhea* sp. nov. (Salazar et al. 1988; Fig. 1), and it may be related to *A. geryon* Felder & Felder of the Cordillera Central and *A. phasiana* Butler, the three taxa perhaps being conspecific (Lamas cited in Salazar et al. 1998).

Of the 21 *Antirrhea* species mentioned by D'Abrera (1984), only the life cycle of *A. philoctetes* (Linnaeus) has been published (Urich & Emmel 1990), and then without any information on the behavior of the larva. Müller (1866) describes the egg and the first instar of *A. archaea* Hübner and notes the resemblance between this and the corresponding instar of *Morpho achillides* Felder & Felder. DeVries et al. (1985) examined the cladistic relationships between the genera *Antirrhea*, *Caerois*, and *Morpho* using larval characters of *A. pterocopha* Salvin & Godman, *A. miltiades* (Fabricius), *Antirrhea* sp. nov., and *A. philoctetes*. We here contribute the first descriptions of clutch size, morphology and behavior of the immature stages, pupal dimorphism, hosts, and potential fertility of *Antirrhea weymeri*, and corroborate the close phylogenetic relationship between *Morpho* and *Antirrhea* proposed in DeVries et al. (1985) and DeVries (1987).

MATERIALS AND METHODS

The study area (1900–2200 m, 3°32′23″N, 76°36′16″W) is 4 km north of "El Dieciocho" (km 18 of the Cali-Buenaventura highway) on the road to Pavas, on the eastern slope of the Cordillera Occidental, municipality of Cali, Departamento del Valle del Cauca. Ecologically, the zone is "lower montane moist forest" of Holdridge's Life Zones system (Espinal & Montenegro 1963). The vegetation consists of patches of more or less degraded cloud forest within suburban estates devoted to recreation or low-intensity forestry and livestock raising.

On 19 August 2001, in a patch of secondary forest bordering the Aguaclara creek we discovered five *Antirrhea weymeri* larvae clustered near the middle of the abaxial surface of one of the pinnae of a young palm (*Prestoea acuminata* [Willd.] H. E. Moore), with leaves approximately 2 m long. Six species of Arecaceae have been recorded in the study area (J. Giraldo pers. com.), and juvenile hosts of *A. weymeri* had the physiognomic characteristics of *Prestoea acuminata*. It was possible to confirm the host identification by comparing the young plant with *A. weymeri* larvae with a nearby adult in fruit. This palm species inhabits Andean pre-montane and montane forests from Colombia to Bolivia, and lower altitudes in Central America and the Antilles (Henderson et al. 1995).

The larvae were transferred to the laboratory in Cali

TABLE 1. Morphometric characteristics of *Antirrhea weymeri*, in millimeters, standard deviation in parentheses.

	3rd Instar	4th Instar	5th Instar
HEAD CAPSULE	n = 5	n = 4	n = 3
width	2.63 (0.027)	3.76 (0.62)	5.55 (0.49)
height	3.06 (0.054)	4.46 (0.047)	5.66 (0.28)
SCOLI			
width	0.23 (0.027)	0.31 (0.025)	0.47 (0.03)
height	0.26 (0.022)	0.27 (0.028)	0.3 (0)
separation at the base	0.16 (0.021)	0.26 (0.025)	not measured

to follow their life cycle. Larvae and pupae were kept in glass jars at a controlled temperature not above 24°C with a 12L:12D photoperiod. Larval food (*P. acuminata*) was changed daily and maintained fresh in moist paper under refrigeration, or replaced with fresh field collected material.

The early stages were described and measured in vivo using a stereomicroscope (15–20×) equipped with 0.1 and 0.05 mm precision grids (Table 1, Fig. 4). The epicrania, a fourth instar larva, some pupal exuviae, and the adults are at present deposited in the private collection of MDH.

RESULTS

Egg. (Fig. 2A) We found the remains of clutches on the abaxial surface of pinnae of young palms, but not on adult palms that were carefully surveyed with binoculars. Eggs were white, hemispherical, laid in small clusters of 5–8 (mean = 5.8, SD = 1.30, n = 5), in most cases in contact with each other, and positioned towards the middle of the leaf. Three eggs with hardly any of their opercular dome consumed measured 1.75 mm in diameter and 1.20 mm in height. Eggs were positively identified by comparison with mature eggs obtained by dissecting newly emerged females in the laboratory.

Third instar. The larvae were at the end of this instar at the time of collection. **Head:** (Table 1, Fig. 4) triangular, with two very close scoli at the vertex, terminating in three forward-pointing setae, one anterior and two posterior. Anterior seta dark brown, and longest and largest in diameter. One posterior seta is dark and intermediate in diameter and length, the other light brown, thinner and shorter. Epicranium cream-colored with a dark brown patch extending transversally between stemma IV longitudinally to the first third of the epicranial suture; its shape is trapezoidal and leaves the interior of the frontal triangle with no coloring. Laterally, there is a dark brown semicircular patch that runs in line with stemma V to the posterior edge of the epicranium. There are small dark brown marks between the first four stemmata and stemma VI at the beginning of another posterior-pointing patch. The edges of the mandibles and the base of the clypeus are dark brown. Cutting edge of the mandibles is uniformly curved, and the mandible wrist is papillate. Cuticle of the epicranium presents tiny circular pits over its entire surface, including the scoli, but excluding areas of the frontoclypeus, adfrontal, and regions close to stemmata and mandibles. The entire cuticle is uniformly spotted with tiny pinacula from which arise fine golden setae; in areas near the mouth and stemmata these setae are longer and supported on minute chalazae. Laterally, there are prominent chalazae from which arise thick, forward-pointing, dark brown setae of different sizes; viewed in profile, most are slightly curved; the shorter occur singly along the edge of the lateral brown-colored patch and extend to the end of the frontal trapezoidal coloration. Some short setae are scattered among the long setae. Several long lateral setae are flat, in the form of small ribbons narrowing towards the ends. On the vertex there are only thick setae of the scoli and one seta anterior to these on a chalaza. Stemmata are all approximately equal in diameter; stemma VI is slightly posterior to V. **Body:** segments with annulets: A1 has three rings, one anterior (cephalic) broader, and two posterior narrower but equal in size; from A2 to A7 there is one broad anterior and four narrow posterior rings equal in size; A8 to A9 lack defined rings. A broad black dorsal band with a yellow subdorsal band on each side and a pattern of dorsal V's distributed from thorax to A6 with vertices at midline. The yellow lateral band touches a narrow black band that is followed by a light green lateral area and a supraspiracular cream line. Ventrally light green with a dark ring around the T1 leg. Suranal plate bifurcate with two long, white-spotted, black prolongations covered with numerous scattered secondary setae. Laterally, the larva presents a great quantity of long, white, downward-pointing secondary setae; dorsally one only sees a few, scattered long and white setae. The duration of this instar not observed; duration of the pre-molt was one day.

Fourth instar (Fig. 2B) Newly molted length 21.90 mm (SD = 0.90, n = 5) not including the suranal plate; suranal plate 11.36 mm (SD = 0.26, n = 5). **Head:** approximately the same width as the body, with the same setal pattern and coloring as previous instar (Table 1), but now frontally beneath the scoli there are several long, thick, dark brown setae, and a greater density of thin golden setae

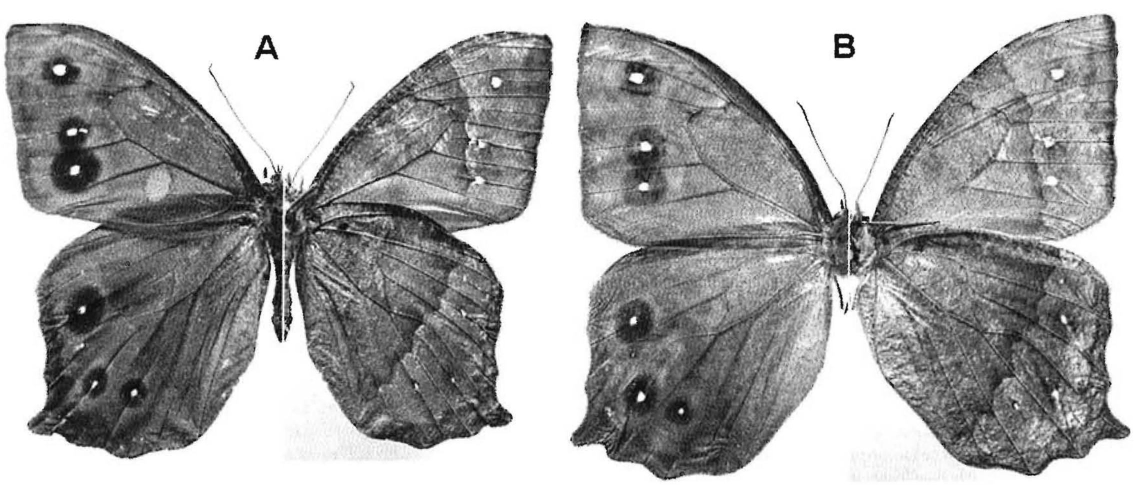

FIG. 1. *Antirrhea weymeri*. **A,** Male; left, dorsal view; right, ventral view. **B,** Female; idem.

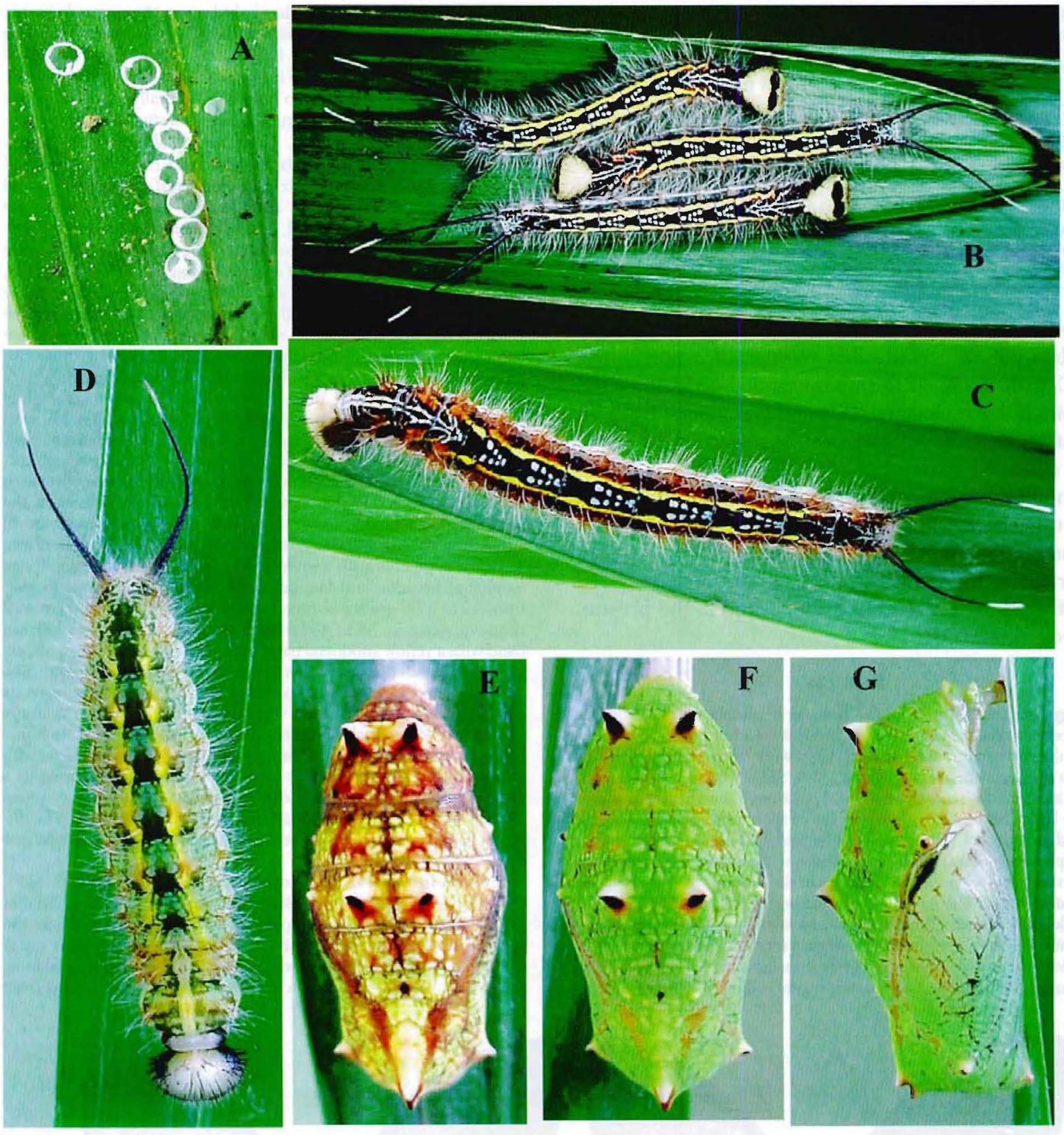

FIG. 2. Immature stages of *A. weymeri*. **A,** Remains of clutch in *Prestoea acuminata*. **B,** Fourth instar. **C,** Fifth instar. **D,** Prepupa. **E,** Dark pupa, dorsal. **F,** Light pupa, dorsal. **G,** Light pupa, lateral.

over entire frontal surface. **Body:** (under 10× magnification) many long, whitish, downward-pointing setae are seen, distributed mainly over the subspiracular region, but there are also scattered long (1.5–2.0 mm), whitish secondary setae over the entire body. There also appear small clusters of shorter (0.8 mm) brown setae mixed with the white on the T2–T3 subdorsal region (setae in this region are forward-pointing as in *Morpho* on verrucae), and from A1 onwards these setae are shifted slightly towards the supraspiracular region; on A3–A4 very sparse, and on A5–A9 they again are dispersed and more numerous; all these setae appear barbed under 40× magnification. Suranal plate with two long, white-spotted, black prolongations covered with numerous, dispersed black secondary setae; those at basal end are white and longer (1.20 mm) except for those on apex which are white and very short. Body with a dorsal black band edged with a thin golden yellow strip running from end of T3 to the beginning of A7 on subdorsal region. This strip is slightly broader at the anterior edge of each segment. Some reddish brown marks anterior to the yellow strip of T3 and the broad ring of A1. Two parallel white lines run along the center of the black dorsal fringe from T1 to middle of first ring of segment A1, at which point they pass around two small fissures, one on each side of midline (see Fig. 3B). These fisssures are in the same position as the tufts on segment A1 in *Morpho sulkowskyi* Kollar and other species of *Morpho*, and suggest they might have the same glandular function. At these fissures there begins a series of white spots, one on each side of each ring, forming a V pattern with vertex at midline, continuing to A6, at

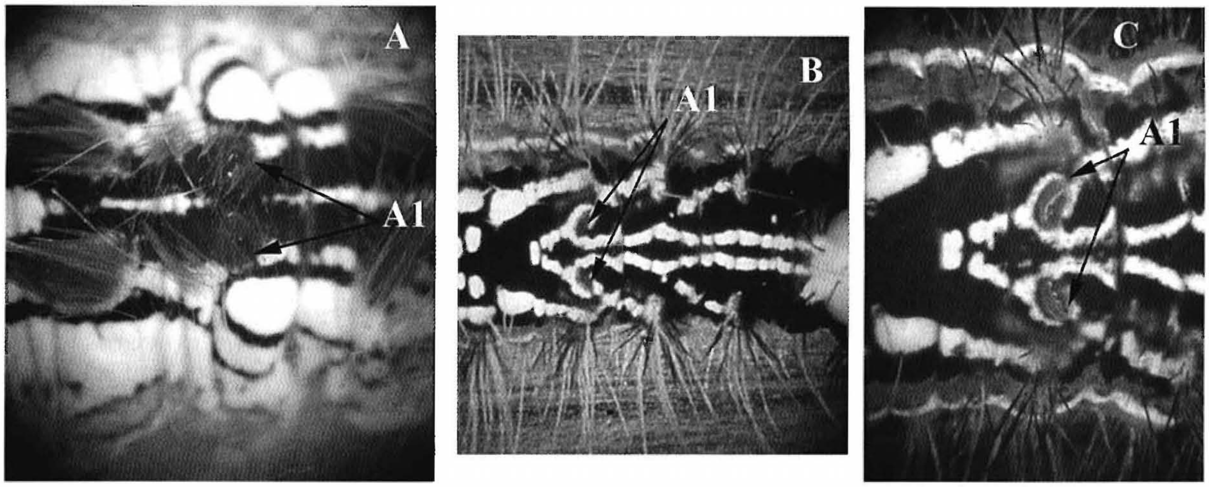

FIG. 3. **A,** *Morpho sulkowskyi*, two drops of secretion on A1. **B,** *Antirrhea weymeri*, two fissures on A1. **C,** Larva of *A. weymeri* on molt to fifth instar showing swollen fissures.

A7 it becomes a thin line parallel to the end of the segment. At A8 and A9, there are scattered dorsal pale cream patches. The lateral yellow band touches a black band with brown highlights, and ventrally there is a transparent green band, then a supraspiracular white line. Spiracles brown. Ventral region transparent green; around the front legs a burgundy-colored ring embracing the light green prothoracic gland region. The mean duration 10.75 days (SD = 0.5, n = 4). One larva died. The pre-molting period, two days.

Fifth instar (Fig. 2C) Newly molted length 29.9 mm (SD = 0.14, n = 4) not including the mean length of the suranal plate (11.5 mm, SD = 0.40). **Head:** (Table 1) same setal pattern and coloring as previous instar, but now scoli are thicker while maintaining the same length. **Body:** coloring basically the same as previous instar, but larva now has a chocolate brown tint. Yellow band has brown inclusions along its length, as does the blackish band following it; greenish lateral band now brown, more intense on edges that touch the cream line. There are also clusters of short brown setae on all segments (except A10) distributed transversally from subdorsal lines to supraspiracular region. Within each segment from A1 to A7, the setae form two parallel rows; A8 to A9 have only a single row. When in two rows the anterior is denser in brown setae and occurs after the broadest ring in each segment. The densest short brown tufts correspond to segments T2–T3, A1, and A8. Dorsally and laterally, above the supraspiracular region there are widely-spaced, long, thin white setae that are most abundant on subspiracular region, and point downwards. Ventrally identical to previous instar. **Prepupa** begins when brown coloration disappears between subdorsal and supraspiracular area which then becomes greenish; subsequently, the entire surface becomes greenish with only the central black area between the pattern of V's that have expanded while still being bordered by the yellowish band (Fig. 2D). Mean prepupa duration 2.5 days (SD = 0.57, n = 4) and the complete fifth instar 21 days (SD = 2.44, n = 4). Larvae disperse towards the end of this instar, and pupate alone.

Pupa. (Figs. 2 E–G) Mean length 19.55 mm (SD = 0.26, n = 4), width 8.92 mm (SD = 0.41). The broadest segment measured laterally coincides with beginning of A3. There were two coloring types: three of the pupae were an intense light green (almost phosphorescent) and one had a yellowish background color strongly marked with brown. Dorsally, the texture of the pupa is granular, with pyramidal protuberances on each side of midline on A3 and A6. Upper part of protuberance is yellowish cream, the lower brown with a black patch. There is a slightly smaller lateral protuberance at the base of the wing, another two connected to form an M on the keel of T2, and finally two much smaller ones beside spiracle A4, and the other on the spiracle A3. A brown stripe corresponding to part of the outer edge and the inner edge of the wing extends to the keel. Spiracles brown. On both A4 and A5 a slanted brown stripe extend each side toward the midline. A prominent dilatation between A4 and A5 that allows lateral movements of the pupa when it is disturbed. Background green color is marked with small stripes or minute dots of light brown. A9 has a dorsal ledge of tiny protuberances. Cremaster with tiny protuberances on each side of base, but ventrally they are less perceptible. Cremaster slightly longer than wide, fluted dorsally and ventrally; hooks brown; silk white. Ventrally two minute brown-apexed protuberances on epicranium separated by 2.5 mm. Small dark brown patch in the proboscis area. Wing discal cell and veins with diffuse light brown markings. Submarginal area with small brown stripes and tornus with a dark, nearly black, elongated patch. Background yellowish green color lighter ventrally.

In light-colored pupae there were individuals with the brown band along the outer and inner edges of the wing to the keel of T2 very dark, and with wings having a great profusion of ventral spots and stripes. Dorsally, the **brown pupa** was chocolate brown from the cremaster to A5 except for light upper part of the A6 protuberances. The dilatation between A4 and A5 also brown, with slanted brown bands on A5–A4. In these segments the background color is somewhat more yellowish than other segments, but with a greater concentration of brown marks (spots and stripes) on the background color. The band around the inner margin of wing to the keel is dark brown and broad. Ventrally greenish cream with a pattern of small stripes, spots and patches darker brown than in the light-colored pupa. Mean duration of pupa, 16 days (n = 4, SD = 0.86).

Larval behavior. Larvae always consumed the molt, and occasionally the tips of the suranal plate. When handled some expelled an oral drop of greenish liquid. As in *Morpho*, larvae had a prothoracic gland and the same associated behavioral repertoire: they push the head back, lift the legs, and move the head from side to side, at times emitting a scent from the cream-colored prothoracic gland, and occasionaly they also lifted the suranal plate and pushed it forwards, lifting the prolegs on the last segment. The scent of the prothoracic gland is not as intense as in some *Morpho*. We observed that larvae were more sensitive to any disturbance immediately following molt.

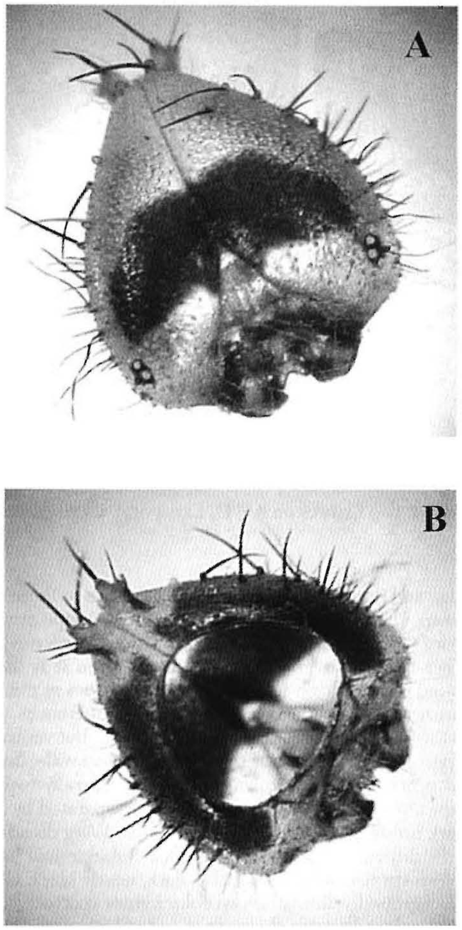

FIG. 4. Head capsule of *A. weymeri*, third instar. **A,** Dorsal view. **B,** Ventral view.

Using 40× magnification we observed three larvae during the pre-molt period slightly extrude the fissures of A1 leaving a smooth swollen light green surface (Fig. 3C). In one larva observed with stereomicroscope while molting, a small drop of a transparent secretion was seen on the rounded surface of the fissures, much like those of the A1 tufts in *M. sulkowskyi* (Heredia & Alvarez-López in press, Fig. 3A). *A. weymeri* larvae also have the same grooming behaviour as described by DeVries and Martinez (1993) for *Morpho* larvae.

A newly molted larva pushed its head back and moved T2 and T3 setae over segment A1. It then turned its head towards the last segments, running first down one side and then the other. The larva performed this sequence even if there was apparently no drop of secretion available to anoint the lateral setae, i.e., all newly molted larvae behaved in the same way, with or without secretion.

Reproductive potential. Two females (wing lengths 34.3 mm and 38.4 mm) were dissected the day following emergence. Both had a great amount of fat body. At the base of each ovariole, the first egg was chorionated and ready to ovulate into the oviductus lateralis. The following two eggs in both females were vitellogenic, large in size, and about to receive the chorion. In one female there were 11 eggs in formation per ovariole, plus eight chorionated, for a total of 96 potential eggs. In the other, there were 12 eggs in formation per ovariole plus eight chorionated (total 104 eggs). The infertile chorionated eggs ranged in size between 1.65 and 1.70 mm in width, and 1.15 mm in height. They were hemispherical and smooth textured.

DISCUSSION

Adults of *A. weymeri* have a behavior similar to that described for other *Antirrhea* species (DeVries 1987, DeVries in D'Abrera 1984, Urich & Emmel 1990, Salazar et al. 1998, and pers. obs.), and also use Arecaceae host plants. *A. weymeri* shares morphological aspects of eggs, larvae, and pupae with the other *Antirrhea* species for which something is known (DeVries 1987, Urich & Emmel 1990), and the main differences appear to be in clutch size and color patterns of larvae and pupae.

The larvae of *Antirrhea weymeri* are gregarious and have prothoracic and grooming glands like those described for *M. cypris* Westwood (DeVries & Martinez 1993) and *M. sulkowskyi* (Heredia & Alvarez-López in press). When disturbed, larvae of *A. weymeri* extrude their prothoracic gland and emit a scent, but this response is more rapid immediately following molt. However, in our experience with *M. sulkowskyi* the prothoracic gland scent is produced at all times with the same rapidity.

The secretion of the grooming gland was first described by DeVries and Martinez (1993) for *Morpho cypris* as "a drop of clear liquid from a dorsal pore located between the subdorsal tufts on A1." In *M. sulkowskyi* (Heredia & Alvarez-López in press) the secretion appears as two independent drops, one for each A1 tuft, implying the existence of two pores (Fig. 3A). Likewise, *A. weymeri* has two small fissures on each side of the midline (Fig. 3B, C) in the same position as the A1 tufts of *M. sulkowskyi*. However, histological studies are needed to confirm the glandular nature of these structures and to compare them with the corresponding structures of *Morpho*. This paper represents the first observations on the behavior and glands of *Antirrhea* larvae (C. Penz pers. com.), and lends support to the phylogenetic placement of *Antirrhea* within the Morphinae (DeVries et al. 1985).

The larval regurgitation, gregarious behavior, and glands with their associated behavioral repertoire may have a defensive function against predators or parasitoids (DeVries & Martinez 1993, Gross 1993, Fitzgerald 1993, Heredia & Alvarez-López in press), but we have no observations on such interactions. In our study area *Antirrhea weymeri* is rare with an erratic presence; indeed, a search for over 10 months yielded no more larvae, despite checking many *Prestoea acuminata* individuals.

Color dimorphism of pupae has been explained as the result of genotype-environment interaction, where production of a green or a brown pupa depends on environmental signals received by the prepupa, and on its genetic capacity to respond (Hazel & West 1979, Sims & Shapiro 1983). In natural conditions *Antirrhea weymeri* very possibly pupates not only on palm leaves, but on many substrates, and this may favor pupal dimorphism and crypsis (West & Hazel 1982).

Nothing is known about the egg production patterns in butterflies that feed on juices from rotting fruit, tree exudates, fungi, or animal droppings. This group, to which *Antirrhea weymeri* belongs, in many places in the tropics may represent 50 % of the butterfly fauna (DeVries 1988, DeVries & Walla 2001, and pers. obs.). From the dissections of two females, we conclude that females could begin to lay eggs soon after copulation since they are born with a group of chorionated eggs and another one of advanced vitellogenic eggs. They would not depend on feeding immediately, nor on copulation for their eggs to begin maturing (Ehrlich et al. 1978). Instead, the availability of food resources for the female could be important subsequently for the remaining eggs to mature (Boggs 1997). This preliminary information is necessary to begin to understand the reproductive strategies of such species as *A. weymeri*, many of which have small populations and very particular environmental requirements making them highly vulnerable to habitat destruction.

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