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BIOLOGY OF *DALCERIDES INGENITA* (LEPIDOPTERA: DALCERIDAE)

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ABSTRACT.– Observations on the biology of *Dalcerides ingenita* (H. Edwards) are documented, many for the first time, with photographs and images captured from video. Dalcerid larvae have a dorsum covered with gelatinous warts. It is reported here that the head, prothorax, ventrum and anal segment of larval dalcerids are molted apart from the dorsum of the remaining thorax and abdomen. The gelatinous warts are irregularly molted and are believed to form as a result of secretions beneath old layers of integument. Time-lapse photography of cocoon construction indicates that the warts are sloughed off and fed on by the prepupa. Images of other behaviors include larval locomotion and use of the spinneret, cannibalism of unhatched larvae by newly hatched siblings, and adult emergence and copulation.

KEY WORDS: *Acraga*, Aididae, Arizona, Brazil, Colombia, Diptera, eggs, Epipyropidae, Ericaceae, Fagaceae, Fulgoroidea, Homoptera, hostplants, Hymenoptera, immatures, larvae, larval behavior, life history, Limacodidae, Megalopygidae, Mexico, Nearctic, Neotropical, parasites, *Prolimacodes*, pupae, South America, Tachinidae, Texas, USA, Zygaenidae.

Dalceridae (84 spp.) are a small, mostly Neotropical group closely related to Limacodidae (Miller, 1994; Epstein, 1996). Lepidopterists have been intrigued by unusual aspects of dalcerid larvae. Their dorsum, coated with sticky gelatinous warts, is exceptional in Lepidoptera caterpillars (Epstein *et al.*, 1994). Hopp (1928) suggested that dalcerid larvae molt the head, ventrum, and rectum apart from the dorsum. This was based on observations that the larvae haphazardly molt the dorsal warts, rather than actually seeing them molt the ventrum. While the gelatinous warts in Dalceridae have been considered homologous to verrucae found in Zygaenidae and Megalopygidae (Hopp, 1928:285) or unassociated with named setae (Stehr and McFarland, 1987), Epstein (1996) determined that fleshy primary setae beneath the warts are homologous to those found in some first instar limacodids. These setae have been referred to as tubercles (Epstein, 1996) or as inner tubercles (Stehr and McFarland, 1987). Likened to that of a slug, the sticky secretions found in the warts serve as a physical deterrent to ants (Epstein et al., 1994; A. Aiello LOT 80-048).

The highly flexible cuticle, abdominal suckers of the ventrum and wavy locomotion of larval Dalceridae are each shared with Limacodidae (Epstein, 1996; Epstein, in press). Several species of dalcerids and a primitive genus of limacodids develop crochets in later instars (Stehr and McFarland, 1985; Epstein, 1996). *Dalcerides ingenita* (H. Edwards) has 6 or 7 instars (Stehr and McFarland, 1985). The appearance of crochets on abdominal segments 3 (A3) through 6 (A6) is delayed until the third instar, while crochets on A2 and A7 are added in the penultimate instar (Stehr and McFarland, 1985). Cocoon construction has been described in other dalcerid species (Lourenção and Sabino, 1994), but without a detailed temporal account of the various stages until adult emergence.

Dalcerid larvae are hosts to a restricted number of parasitic families. Many of the recorded species of Hymenoptera appear to be hyperparasites, while many Diptera are in *Pararrhinactia* (Tachinidae) (Miller, 1994). There have been scattered reports on the biology of dalcerid species reported as pests (e.g., Genty *et al.*, 1978).

The purpose herein is to document new or poorly known aspects of dalcerid behavior and biology, with *Dalcerides ingenita* as an exemplar. These include egg eclosion and cocoon construction, as well as feeding, locomotion, silk use and the occurrence of partial molting in the larva.

MATERIALS AND METHODS

Larval behavior of *Dalcerides ingenita* was observed with the aid of 8 mm camcorder, or video taped through the ocular of a stereo microscope, or with a video hookup to an inverted phase contrast compound microscope. Video images were captured with a frame grabber (Sony Still Video Recorder). Larvae were reared from eggs laid by one female within a plastic bag in May 1993 from Ash Canyon, 1570m, Huachuca Mountains, Cochise Co., Arizona. Cocoon construction was observed by camcorder and time-lapse photography using a 35mm camera with a flash and a macro lens. The 35mm camera took frames every 2 minutes for the first 4 hours, every 5 minutes the next 3 hours and every 30 minutes overnight and for the next 24 hours until the completion of the cocoon. The photographs were taken from above through a sheet of glass, with the prepupa spinning between the leaf and the glass.

FRONTISPIECE: Color variation in ultimate instars of *Dalcerides ingenita*. Late stage dalcerid caterpillars do not aggregate under natural conditions (photo by Laurie Minor-Penland).

Fig. 1-3. Copulation and eggs of *Dalcerides ingenita* (photos by Carl Hansen): **1**. Copulating pair (male above left). **2**. Eggs on manzanita. **3**. Larva hatching from egg (left) and newly hatched larvae (right).

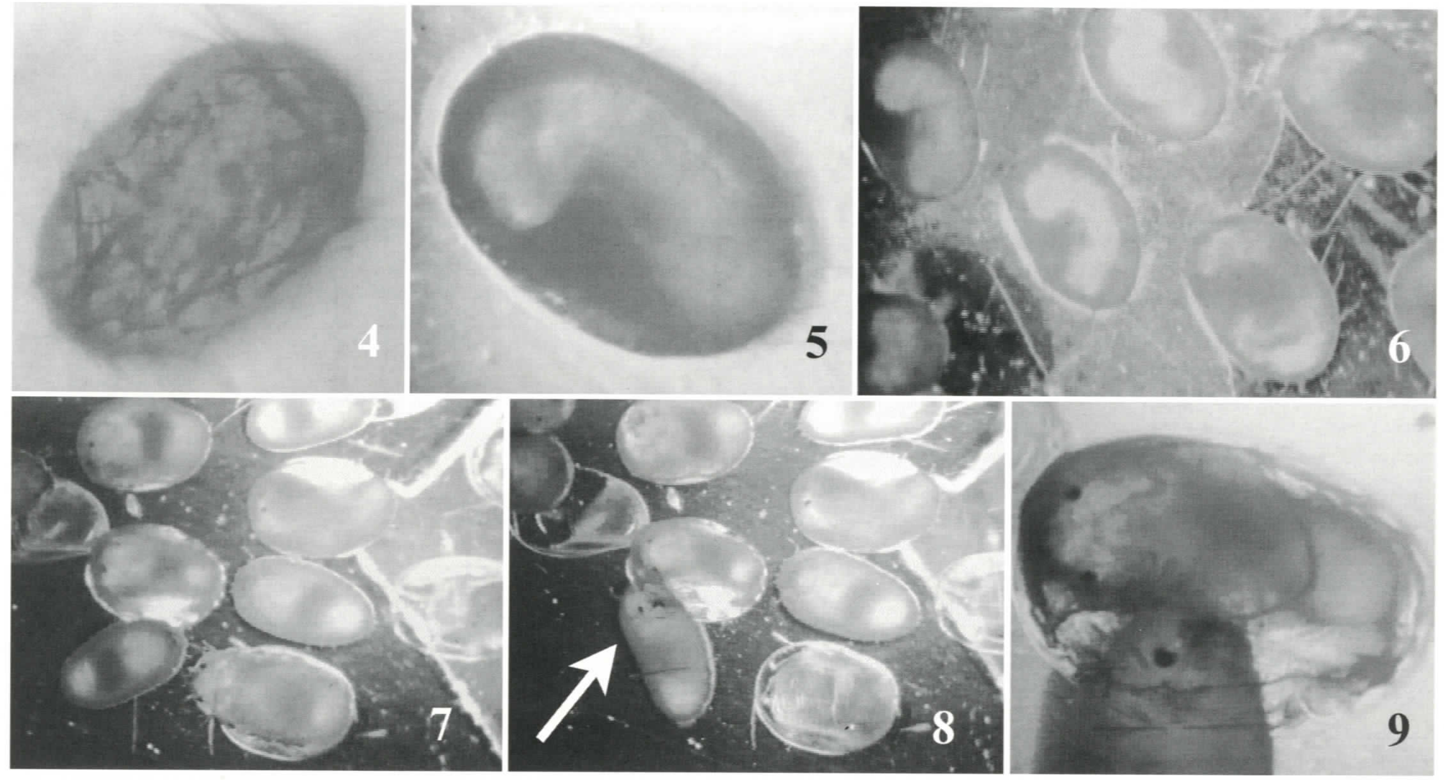

Fig. 4-9. Eggs, embryos and newly hatched larvae (from video): **4**. Egg viewed from above (dark patches are scales from female). **5**. Egg viewed from below with visible embryo. **6**. Group of eggs/embryos from below. **7**. Egg hatching (center below). **8**. Newly hatched larva from Fig. 7 feeding on unhatched larva (arrow). Fig. **9**. Closeup of larvae from Fig. 8.

BIOLOGY OF *DALCERIDES INGENITA*

Dalcerides ingenita occurs in northern Mexico, southern Arizona and Texas, making it the sole species of the Dalceridae to occur in the U.S. (Miller, 1994). In the Huachuca Mts., southeast Arizona, adults fly from late April until late September, with the spring brood usually ending in June and the second brood from mid July to late September (Stehr and McFarland, 1987; Noel McFarland, pers. comm.). Male *D. ingenita* are reportedly on the wing from midnight to an hour after sunrise, while females are nocturnal and are attracted to blacklight throughout the night (Stehr and McFarland, 1987; Miller, 1994). A pair from the second brood was observed to copulate during the daylight morning hours in a rearing cage (Fig. 1). Native hostplants reported for the larvae include manzanita, *Arctostaphylos pungens* (H.B.K.) (Ericaceae), and oaks *Quercus emoryi* Torrey and *Q. oblongifolia* Torrey (Fagaceae) (Stehr and McFarland, 1987; Miller, 1994).

Dalcerides ingenita appears to overwinter in the larval stage. I observed larvae, which arise from the second brood, to diapause as early instars in August after feeding. Although under laboratory conditions these larvae did not survive the winter, in nature the larvae of *D. ingenita* are likely to resume feeding in the winter. This is suggested by the report of a mature larva on *Q. emoryi* in the early spring in southern Arizona (Stehr and McFarland, 1987).

Eggs of *D. ingenita* are laid in groups, under laboratory conditions, with individual eggs not touching each other (Fig. 2). This type of group oviposition occurs in other dalcerid species, including *Acraga moorei* Dyar (Lourenção and Sabino, 1994) and *Acraga infusa* complex (Colombia: P. Genty, USNM collection). Coating the eggs is a sticky substance believed to be secreted from a pair of external ducts that arise from large accessory glands (Miller, 1993) and scales from the female abdomen (Fig. 4). Embryos are visible inside the eggs due to the thin chorion (Fig. 5-9), although they are more visible from below through a clear plastic substrate because the sticky coating and the scales cover them above (compare Fig. 4 and Fig. 5).

Dalcerides ingenita larvae eat part of their egg shells while hatching (Fig. 3, 7). I observed some newly hatched larvae to eat their unhatched siblings (Fig. 8-9), although this was under abnormal conditions where the eggs were deposited on clear plastic. It is plausible for cannibalism to occur on the hostplant, as reported for *Danaus* by Brower (1961), because *D. ingenita* lives in a dry habitat and later shows an affinity for eating its own gelatinous warts (see cocoon construction below). Recently hatched larvae lack obvious gelatinous warts on the dorsum (Fig. 3).

The larvae prefer to feed on the underside of old, tough leaves and are negatively phototrophic (Stehr and McFarland, 1987). Window feeding occurs in early instars (Fig. 10-11); on manzanita leaves they are extremely well camouflaged while feeding recessed into the thick leaves because of their small size and translucence. First and second instars were observed to use their mandibles to remove debris stuck to their dorsum and ventrum (Fig. 11). By third or fourth instar the caterpillars feed individually and are large enough to clasp laterally and from front to rear on narrow leaf ends (on oak) or on stems with their sluglike

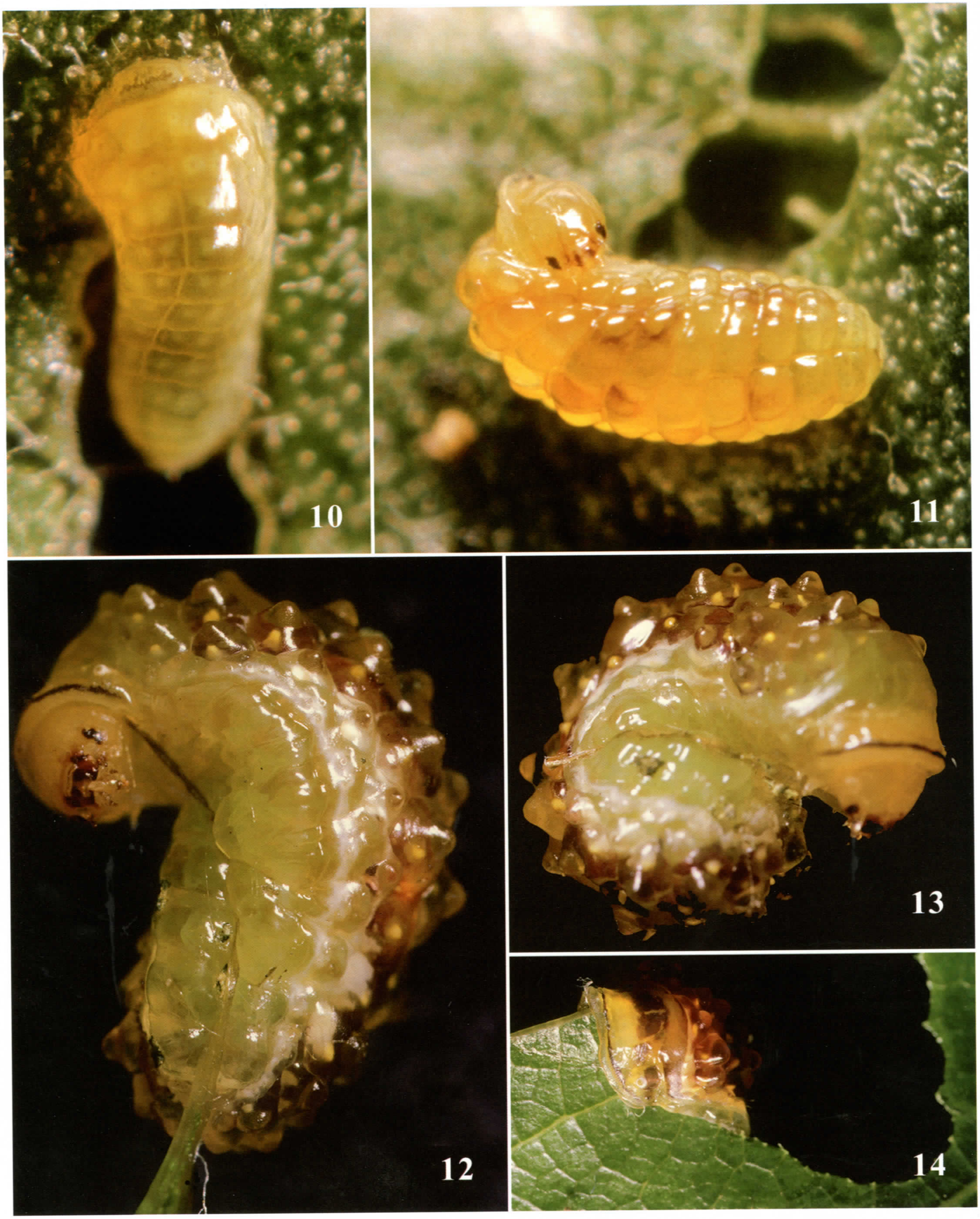

Fig. 10-14. Larval feeding in early instars on manzanita and late instars on oak (Fig. 10-11 photos by Carl Hansen; Fig. 12-14 by Laurie Minor-Penland): **10**. First instar larva crawling out of area it had been feeding on (head end above; note weakly developed gelatinous warts). **11**. Second instar larva preening gelatinous warts with its mandibles. **12**. Late instar larva laterally clasping the leaf end with abdominal prolegs. **13**. Individual from Fig. 12 clasping from anterior to posterior around a leaf end. **14**. Late instar larva feeding along leaf edge with head and mouthparts hidden beneath prothorax.

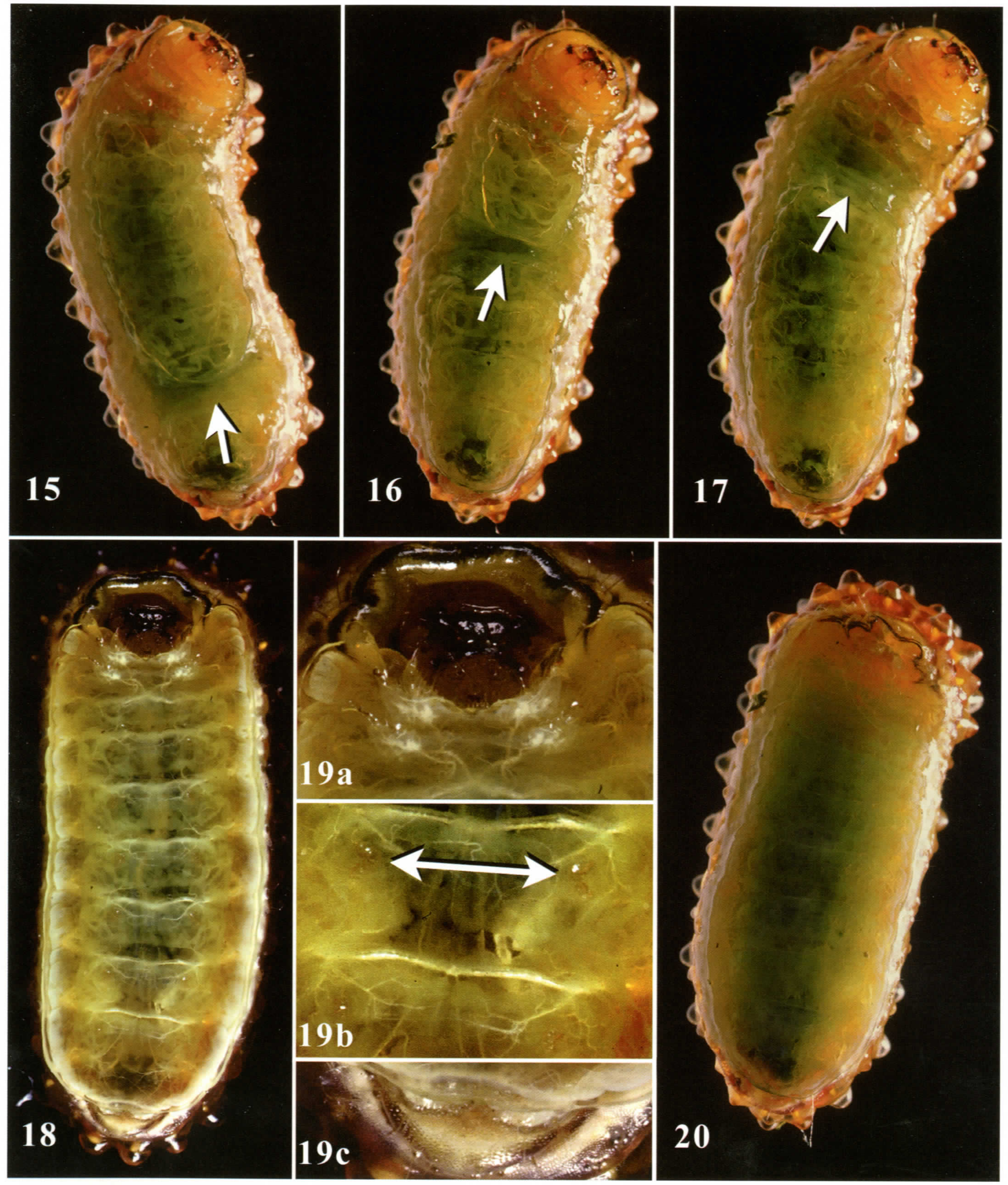

Fig. 15-20. Larval locomotion and ventrum viewed through glass (Fig. 15-17, 20 photos by Laurie Minor-Penland; Fig. 18-19, photos by Frederick W. Stehr): **15-17**. Sequence of locomotion from the beginning to the end of a cycle (arrow indicates leading edge of wave). **18-19**. Larva at rest and head partially retracted (19a-c are closeups of Fig. 18): 19a) Head and tiny thoracic legs. 19b). Abdomen (arrow points to location of crochets on A6; crochets on A7 visible below on the left). 19c) Anal proleg (not in contact with glass). **20**. Larva with head fully retracted.

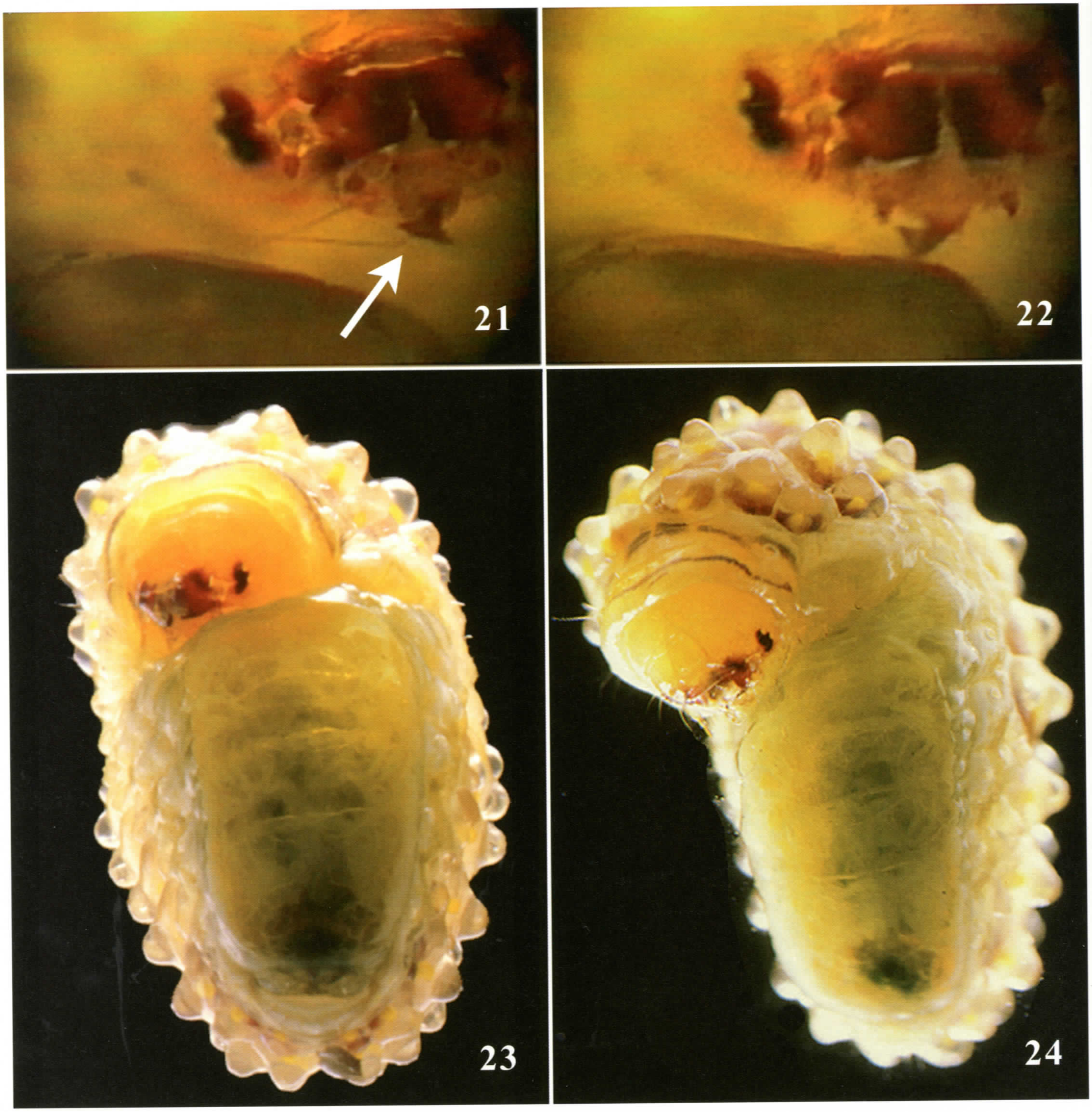

Fig. 21-24. Larva laying down silk and cleaning ventrum with spinneret (Fig. 21-22 from video; Fig. 23-24 photos by Laurie Minor-Penland): **21**. Closeup of spinneret and silk strand (arrow). **22**. Closeup of spinneret brushing against ventrum (either applying silk or cleaning). **23-24**. Larva cleaning or laying silk on ventrum.

ventral surface (Fig. 12-13). At this stage larvae begin to feed on leaf edges, with mouthparts covered by the prothorax (Fig. 14), as occurs in other related families (e.g., Limacodidae and Aididae) (Epstein, 1996; Epstein, 1995). The mouthparts are partially visible because the prothorax is translucent.

The larval locomotion (Fig. 15-17), described in Epstein (in press), consists of undulations of the highly flexible cuticle from posterior to anterior. The anal segment (Fig. 19c), which has rough cuticle without crochets, does not contact the substrate. Viewed from underneath while on glass, the internal organs are visible, especially soon after molting (Fig. 18). The tiny semicircles of crochets, found only in mid to late instars, are difficult to see without the aid of magnification (Fig. 19b). During locomotion the spinneret is held between the labial palpi with the distal end directed to the posterior (face down). At rest a larva may have its head either partially (Fig. 18-19a) or fully retracted (Fig.

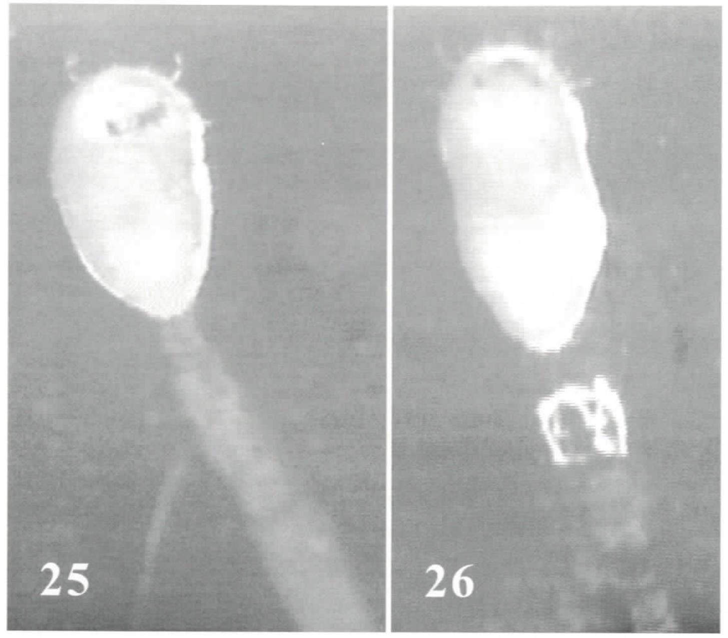

Fig. 25-26. Early instar leaving debris behind after cleaning ventrum with spinneret (from video).

20). In some instances prior to crawling, larvae apply semifluid silk or a secretion along with the silk to the ventrum of the first few abdominal segments by raising the head and front of the body off the substrate and moving their head and spinneret from side to side with head at least partially retracted (Fig. 21-24) (Epstein, 1996; Epstein, in press). The silk or associated secretion, also applied to the substrate, helps the larvae adhere to smooth leaf surfaces, while the broad-tipped spinneret has an added function as a brush to clean off debris stuck to the ventrum (Epstein, 1996; Epstein, in press). An early instar larva was observed to clean with its spinneret and then leave behind a smear of grime as it crawled, apparently loosened by the wet silk or associated fluid (Fig. 25-26). From a stationary position, a larva can also use locomotory waves to assist in removing substances from the ventrum.

Molting of the head and ventrum occurs as the gelatinous warts remain in place on the dorsum (Fig. 27-30) (see discussion below). Prior to molting the larva broadly contacts the substrate, with head retracted (Fig. 20). The larva pulls its head and prothorax (including the tracheal lining of prothoracic spiracles) out of the old cuticle, leaving both fully extended (Fig. 29-30) (D. Murawski, pers. comm.). Also molted are of the ventral thoracic and abdominal portions, including the spiracles and cuticle just below the rows of gelatinous warts of the abdomen, and the setose anal segment. In the final stages the tracheal linings from the abdomen are pulled out as the larva raises up its dorsum (Fig. 30). The old cuticle is left stuck to the leaf.

Although I did not observe larvae to molt clusters of warts on adjoining segments as reported by Hopp (1928), I found warts to be lost at random when larvae brushed against leaves, as described by Zikan (see Hopp, 1928). By pulling off a dorsal gelatinous wart with a camel's hair brush or a glass rod, the neighboring gelatinous warts to each side are also removed (Fig. 31) (Hopp, 1928; Epstein *et al.*, 1994). This is because the warts are all more strongly attached to each other than to warts to the anterior or posterior. The lateral connection between warts may allow the larva to keep more of its protective coating following an attack than if warts were removed in longitudinal bands. After removing the gelatinous coating, yellow tubercles below remain intact (Fig. 32).

In later instars the color of the dorsum varies from cinnamon (Fig. 31) to olive-brown (see Frontispiece). At the beginning of the prepupal stage the larval dorsum turns green, while some individuals have a visible orange patch beneath the cuticle (Fig. 33). I believe this patch to be the nascent secondary accessory gland of the female.

On oak the loosely spun yellowish-white cocoons are constructed on upper leaf surfaces, with the leaf margins curling around them. The following is a summary of cocoon construction, pupation and adult emergence by an individual that began spinning at 0950h on July 14, completing the cocoon approximately 24 hours later: 1) soon after an oval outer chamber was spun the gelatinous warts began to abrade in horizontal rows (Fig. 34); 2) a cast off row of warts was fed upon for at least 22 minutes, although traces of the chafed warts remained throughout construction (Fig. 35); 3) after completion of the outer chamber, the prepupa began construction of the smaller and denser inner chamber, which is approximately the size of the prepupa (Fig. 36); 4) when the cocoon was completed, the confined prepupa no longer had warts due to abrasion and ingestion, as described, and perhaps because of simple desiccation (Fig. 37); 5) pupation took place three days after the cocoon was completed, and the individual remained as a pupa for six days (Fig. 38); 6) the pupa pushed out the side of the inner chamber, where its head was facing, and the adult male eclosed, probably at ca. 1800h on 24 July (Fig. 39).

DISCUSSION

Observations of molting of *D. ingenita* (Fig. 27-30) and of a dalcerid species from Rondonia, Brazil, all support Hopp's surmise that dalcerid larvae molt the ventrum apart from the dorsum (for the Rondonia species, S. Passoa and S. Borkin, pers. comm.; see photograph of this larva by Dan Petr in photo contest section, Fig. 6, *Trop. Lepid.* 3(2), 1992) . The process of partial molting and formation of warts may occur in the following way: 1) from second instar on, the new instar retains, at least initially, the old integument of the previous instar on the dorsum; 2) sticky secretions from tubercles beneath fills the warts, thus giving them their shape (also suggested by Stehr and McFarland, 1987); 3) transverse rows or individual warts can then be either sloughed off through brushing against leaves or are removed by attacking predators (e.g., ants; Epstein *et al.*, 1994); 4) on segments where warts are sloughed off, the integument beneath forms the outer surface of the new warts, which are later expanded by secretions beneath.

The scenario above would explain why newly hatched larvae have barely noticeable warts, in contrast to the warts of the second instar (compare Fig. 3 and 10 with Fig. 11). The occurrence of an integumental component to the warts is supported by several factors, including their structural integrity and their transverse linking when pulled or sloughed off. Furthermore, the

Fig. 27-30. Larvae with freshly molted ventrum and retained dorsal gelatinous warts (Fig. 27 photo by Carl Hansen; Fig. 28-30 photos by Darlyne Murawski): **27**. Newly molted second instar larva (skin of ventrum lower left). **28**. Mid-instar larva with cast skin from head (head not visible). **29**. Mid-instar larva with head and prothorax extended. **30**. Mid-instar with head and prothorax extended, and old tracheal lining beneath ventral surface (same individual as Fig. 28).

smooth surface texture of the warts in first instars (Epstein, 1996) and scaly texture in late instars, as seen through scanning electron micrographs, are similar to those found in some limacodid larvae (e.g., *Prolimacodes badia* Hübner; Dyar, 1896: pl. 7) .

The small pantropical family Epipyropidae have hypermetamorphic larvae, which produce a waxy covering while attaching themselves to Fulgoroidea and other homopteran hosts (Davis, 1987). Jordan (1928) and Hopp (1928) believed that epipyropids were a lineage of dalcerids. As an extension of this concept, Hopp (1928) considered the dorsum and the specialized type of molting in dalcerids to be a preadaptation for the parasitic habits of epipyropids. This hypothesis, however, seems unlikely based on a lack of phylogenetic evidence to support the close relationship between epipyropids and dalcerids (Epstein, 1996). Furthermore, as I stated above, the warts of dalcerid larvae appear to have a cuticular component rather than being a cuticular secretion, such as the wax produced by epipyropid larvae.

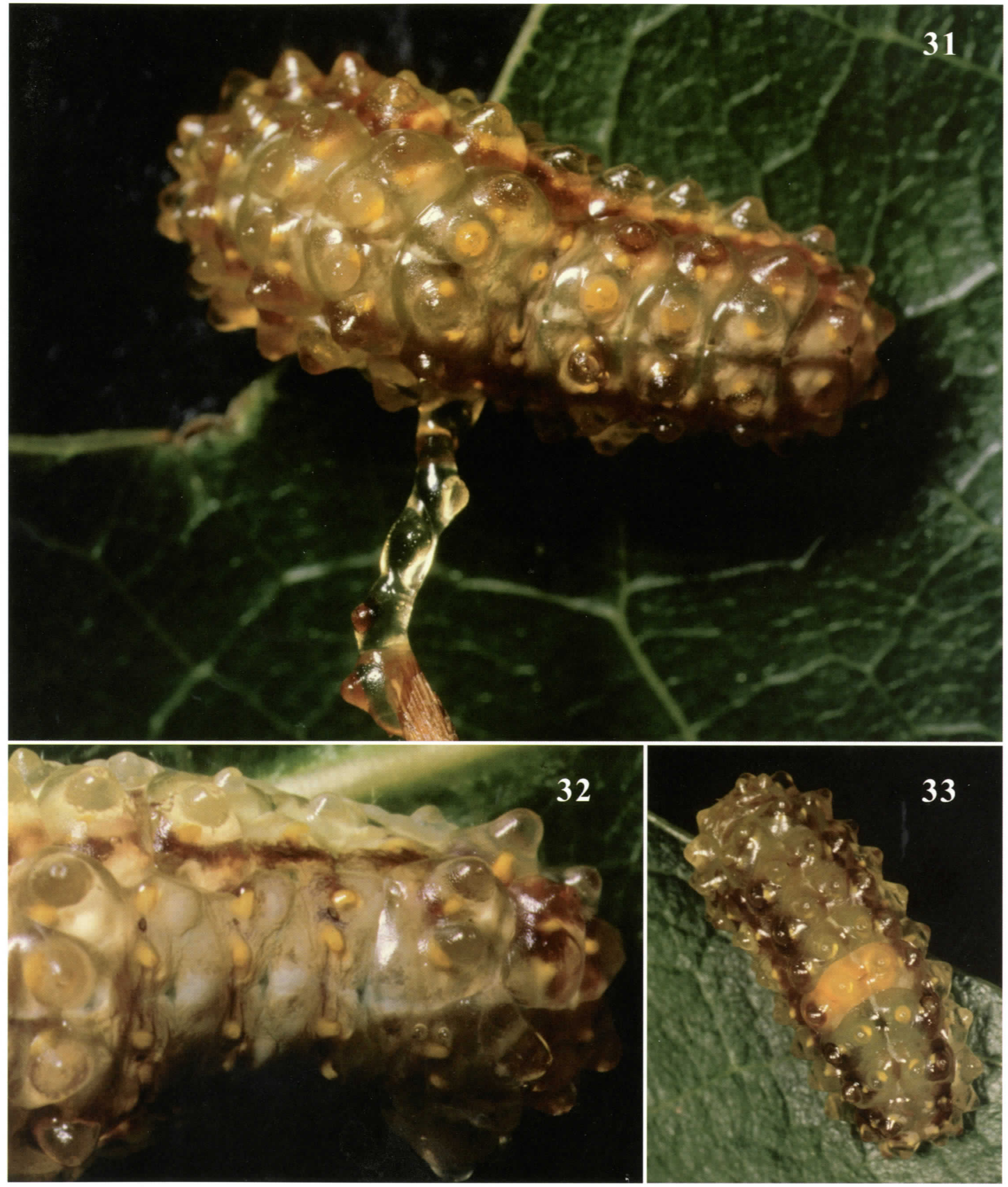

Fig. 31-33. Dorsal gelatinous warts (photos by Laurie Minor-Penland): **31**. Removal of one transverse row of gelatinous warts from the abdomen with a camel's hair brush. **32**. Dorsum with several rows of warts removed and yellow tubercles visible. **33**. Last instar near the onset of cocoon construction as evidenced by it green color; visible orange patch believed to be secondary accessory glands of female.

Fig. 34-39. Sequence of cocoon construction, pupation, and adult emergence (photos by Laurie Minor-Penland): **34**. Initial stages, prepupa spins outer chamber and gelatinous warts begin to slough off. **35**. Prepupa feeds on horizontal row of gelatinous warts (center) (approx. 1 hour after previous figure). **36**. Inner chamber of cocoon nears completion (18 hours after previous figure). **37**. Prepupa has completed spinning cocoon (note loss of warts on dorsum) (28 hours after previous figure). **38**. Pupation occurs at least 5 days after onset of construction (head to left)(photo taken a day before eclosion). **39**. Eclosed pupa (left) that had earlier pushed out of the inner chamber and part of the way out of the cocoon.

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