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Evolution of locomotion in slug caterpillars (Lepidoptera: Zygaenoidea: Limacodid group)

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Abstract. Larval locomotion of species in the limacodid-group families Limacodidae, Dalceridae, Megalopygidae, Aididae, and Somabrachyidae is described in phylogenetic context. Function of structures involved in locomotion reported include thoracic legs, abdominal prolegs or suckers, and spinnerets. Additional segments with prolegs or suckers in the limacodid-group families increase their ventral surface contact with the substrate. The limacodid + dalcerid clade has the most fluid waves of locomotion because of a highly flexible ventrum, tactile lateral setae and size reduction of prolegs and thoracic legs. On flat surfaces aidids have a similar locomotion to limacodids due to short prolegs and smooth lateral and subventral warts, which contact the substrate, whereas in megalopygids the motion of each proleg segment is more apparent because contact of the substrate is primarily with membranous pads on their prolegs. Ventral adhesion in the limacodid + dalcerid clade is increased by the spinneret both in laying down wet silk and in cleaning debris off the ventrum. Evolution of locomotion and its adaptive significance in the limacodid group are discussed.

Key Words. Limacodid group, larval locomotion, prolegs, crochets, suckers, spinneret, silk, smooth hostplants

INTRODUCTION

External feeding larvae in the moth family Limacodidae are often referred to as "slug caterpillars" because their sticky ventrum and locomotion are superficially similar to those of slugs. Dyar (1899:69) referred to the wave-like motion of their ventral abdominal segments during locomotion as "the creeping disk." Hinton (1955:516) noted that when limacodids crawl, "a liquid is secreted over the cuticle... if not sticky... may function... by increasing the efficiency of the suckers or by surface tension binding the abdomen to the leaf surface." Epstein (1996) found semifluid silk to be a source of this liquid.

Limacodidae is part of a monophyletic assemblage that includes Megalopygidae, Dalceridae, Aididae, and Somabrachyidae that is referred to as the limacodid group. A summary of relationships of the limacodid group, based on cladistic analysis found in Epstein (1996) is as follows: megalopygid subfamilies Trosiinae and Megalopyginae form a clade at the base of the limacodid group, and Aididae, often considered a subfamily of Mega-

lopygidae, is a family and sister group to the Limacodidae + Dalceridae. Somabrachyidae are thought to be a sister group of Megalopygidae, Aididae or to the remaining families in the limacodid group.

Larvae of each family in the limacodid group have prolegs on the second and seventh abdominal segments (A2 and A7), unique in Lepidoptera families with external feeding caterpillars. Megalopygidae are the only family in the group with species that possess well developed membranous pads on proleg segments A2–7. Dalcerids and limacodids have ventral abdominal suckers that are considered to be derived from proleg bases on A2–7, and from warts on A1 and A8 (Epstein 1996).

In this study I present observations on the locomotion found in all limacodid-group families. This is followed by discussion of phylogenetic trends in locomotion in these families as they relate to plants and defense.

MATERIALS AND METHODS

Locomotion was observed with larvae of a variety of instars crawling at all angles on clear glass or plastic, and on wires or stems. Larvae were filmed using a 16 mm movie camera with a macro lens or videotaped, either directly or through a microscope, using an 8 mm camcorder. For larvae crawling on glass, locomotion of the ventrum was recorded from below by using an inverted phase-contrast microscope. Species observed are included in Table 1.

LOCOMOTION

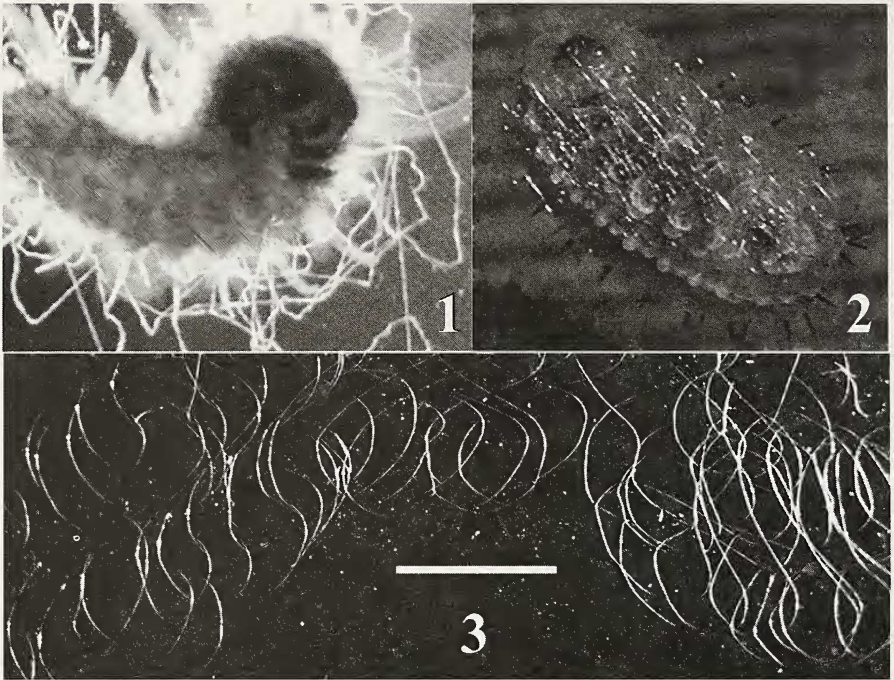
Caterpillars crawl by serial muscle contractions surrounding a fluid skeleton (Casey 1991). Forward motion begins as the anal prolegs, or claspers (A10), are lifted and planted, and continues sequentially with each segment by contraction of dorsal longitudinal muscles of the segment to the anterior; this lifts several trailing segments while dorsoventral muscles retract the prolegs. The prolegs are then set down, beyond their original position, by a contraction of the ventral longitudinal muscle of its segment (Hughes & Mill 1974). Whether in motion or at rest, the amount of ventral surface contact with the substrate of free-feeding caterpillars can be viewed as a

Table 1. Larvae of species in the limacodid group on which observations of locomotion are based in this study.

Limacodidae:	<i>Phobetron pithecium</i> (Abbott & Smith), <i>Isochaetes beutenmuelleri</i> (Hy. Edwards), <i>Tortricidea pallida</i> (H.-S.), <i>Semyra coarctata</i> complex, <i>Prolimacodes badia</i> (Huebner), <i>Isa textula</i> (H.-S.), <i>Acharia stimulea</i> (Clemens), <i>Parasa indetermina</i> (Bdv.), <i>Euclea delphinii</i> (Bdv.)
Dalceridae:	<i>Dalcerides ingenita</i> (Hy. Edwards)
Megalopygidae:	<i>Megalopyge</i> sp. from Belize, <i>Megalopyge crispata</i> (Packard), <i>M. basalis</i> (Walker), <i>Norape cretata</i> (Grote)
Aididae:	<i>Aidos amanda</i> (Stoll)
Somabrachyidae:	<i>Psycharium</i> sp.

Table 2. Morphological characters of the limacodid group and Zygaenidae that relate to locomotion (from Epstein 1996).

Family	Spinnerets	Thoracic legs	Ventral abdominal segments(A1-9): prolegs, crochets or suckers	Anal prolegs (A10): with crochets	Texture of ventral surface, thorax to anal proleg	Lateral surface, setae
Zygaenidae	tubular/normal	easily visible	prolegs on A3-6 with crochets	crochets present	shagreened	lateral and subventral verrucae
Somabrachyidae	"	"	prolegs on A2-7, crochets on A3-6	"	shagreened	"
Megalopygidae	"	"	prolegs on A2-7, crochets on A3-6, or A2-7	"	shagreened except on membranous proleg pads	"
Aididae	tubular with amorphous apex	"	prolegs on A2-7, crochets on A3-6	"	shagreened	lateral warts with tactile setae, subventral warts
Dalceridae	brushlike, broad at apex (all instars)	small	suckers A1-8, crochets absent until mid instars	crochets absent	smooth and flexible	lateral setae tactile, near and above spiracle
Limacodidae	brushlike, often broad at apex (often narrowing after first instars)	small to minute	suckers A1-8, crochets usually absent	crochets usually absent	"	lateral setae tactile, below spiracle



Figs. 1–3. Use of silk in larvae of Somabrachyidae, Aididae, and Megalopygidae. 1) Haphazard laying down of silk of a first instar *Psycharium* sp. (Somabrachyidae), viewed from beneath through glass; 2) Middle instar *Aidos amanda* clinging to glass, viewed from above through glass (photo courtesy of Max and Eileen Price); 3) Figure-8 silk on glass from *Megalopyge* sp. (photo by Kjell Sandved) (scale is in mm).

continuum. Limacodids and dalcerids are at one extreme, with most of the ventrum minus the A10 segment in contact, while the condition commonly found in geometrids, with only thoracic legs and A6 and A10 prolegs in contact, is at the other extreme. Other free-feeding caterpillars fall in between by having a maximum of five prolegs in contact.

Caterpillar locomotion involves a complex of structures, behaviors, and positions in relation to the contact surface. Morphological characters relating to locomotion in each of the limacodid-group families is given in Table 2. These include external aspects of the spinneret, thoracic legs, abdominal prolegs or suckers, anal prolegs, the texture of the ventral surface, and lateral structures.

The descriptions of locomotion in the limacodid-group families are ordered from plesiomorphic to derived taxa based on the phylogeny from Epstein (1996). Somabrachyidae, of uncertain relationship to the other families, is placed after the Megalopygidae. The descriptions include information from these categories: 1) locomotion on narrow surfaces; 2) locomotion on flat surfaces; 3) use of silk and the spinneret; 4) feeding and rest-

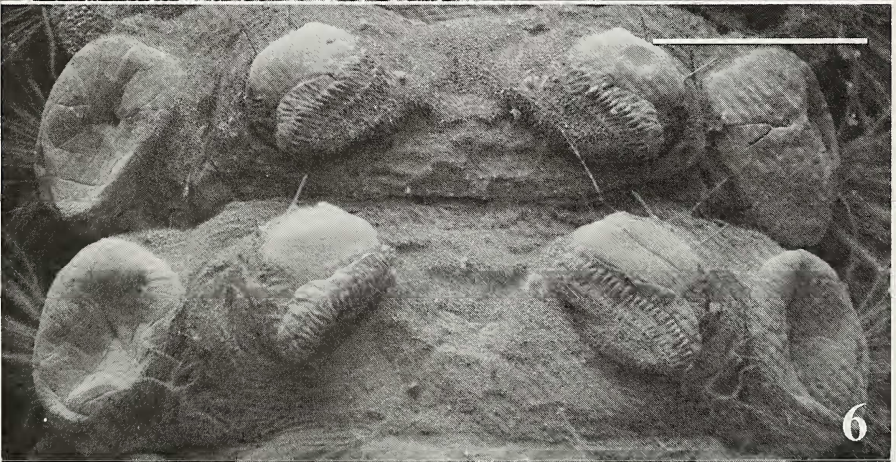
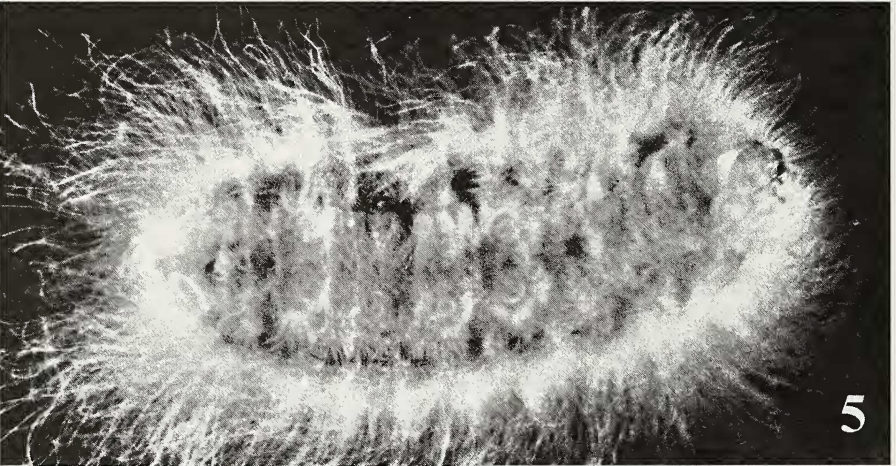
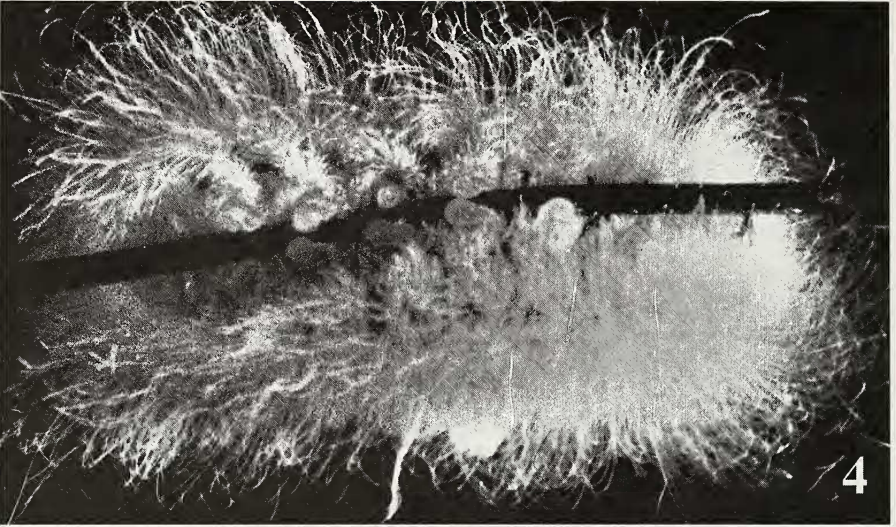
ing positions. For the families for which I have the most information, Limacodidae and Megalopygidae, I will use these categories as subheadings.

Megalopygidae. 1) *Narrow surfaces*: Larvae use thoracic legs and all prolegs, including the anal pair, to grasp (Fig. 4). 2) *Flat surfaces* (Fig. 5): Membranous pads (Fig. 6) are the primary contact of the prolegs on A2–7 (as indicated through glass); a pair of tactile, subventral setae positioned at the anterior margin of each pad touches the substrate. Lateral and subventral verrucae have little contact with the substrate except in certain instances (e.g., *Mesoscia pusilla*). The anterior, non-crochet portion of the anal prolegs contacts substrate at the beginning of a wave of locomotion, while at least two adjoining proleg pairs are retracted (and compressed) from the substrate as the wave progresses. 3) *Silk*: Early instars spin silk on horizontal surfaces in a linear or haphazard manner (as in Somabrachyidae, Fig. 1), and can dangle from silk, while later instars issue silk on the substrate in a figure-8 (Fig. 3), especially when they are at an angle of ≥ 45 degrees. 4) *Feeding and resting*: Larvae cling to silk they deposit on the substrate with their thoracic legs and crochets.

Discussion: Packard (1893) noted that the prolegs on A2 and A7 in *Megalopyge (Lagoa) crispata* functioned like the others, even though they lacked the crochets. Dyar (1899) observed that the membranous pads (=disks) of *Megalopyge opercularis* were in exclusive contact with a smooth glass surface during locomotion. Some species of megalopygids have sucker-like pads below subventral verrucae in addition to the membranous pads on the prolegs (e.g., *Mesoscia pusilla*; Fig. 6). These presumably contact the substrate much the same way as the proleg pads. The size of the membranous pads relative to the prolegs varies between species, and on A2 and A7 depending on whether crochets are present or absent (Epstein 1996).

Somabrachyidae (*Psycharium* sp., first and second instars, only). These larvae prefer to crawl on narrow surfaces such as found on its hostplants (Restionaceae and *Pinus*, H. Geertsema pers. comm.). When viewed from underneath on a glass surface the prolegs sometimes clasped together, as if to grip a narrow substrate, rather than push directly on it. Silk is deposited in the same, haphazard way as in early instar megalopygids (Fig. 1).

Aididae. Movement on flat surfaces of proleg segments has a fluid wave-like appearance similar to limacodid and dalcerid species, because they closely contact the substrate with short, broad prolegs and smooth lateral and subventral warts below the spiracles (Fig. 2). Most megalopygids, in contrast, have only the membranous pads contact flat surfaces, whereas the proleg base and crochets and the spiny and plumose setae on lateral and subventral verrucae have less contact with flat surfaces. The major difference between locomotion found in *Aidos amanda* and in limacodid and dalcerid species relates to the presence of a flexible ventral cuticle found in the latter two families. Larvae of *A. amanda* are difficult to dislodge at rest because they have a large number of crochets hooked onto silk (Fig. 2) (Epstein 1996); they issue silk while crawling onto a leaf or on smooth

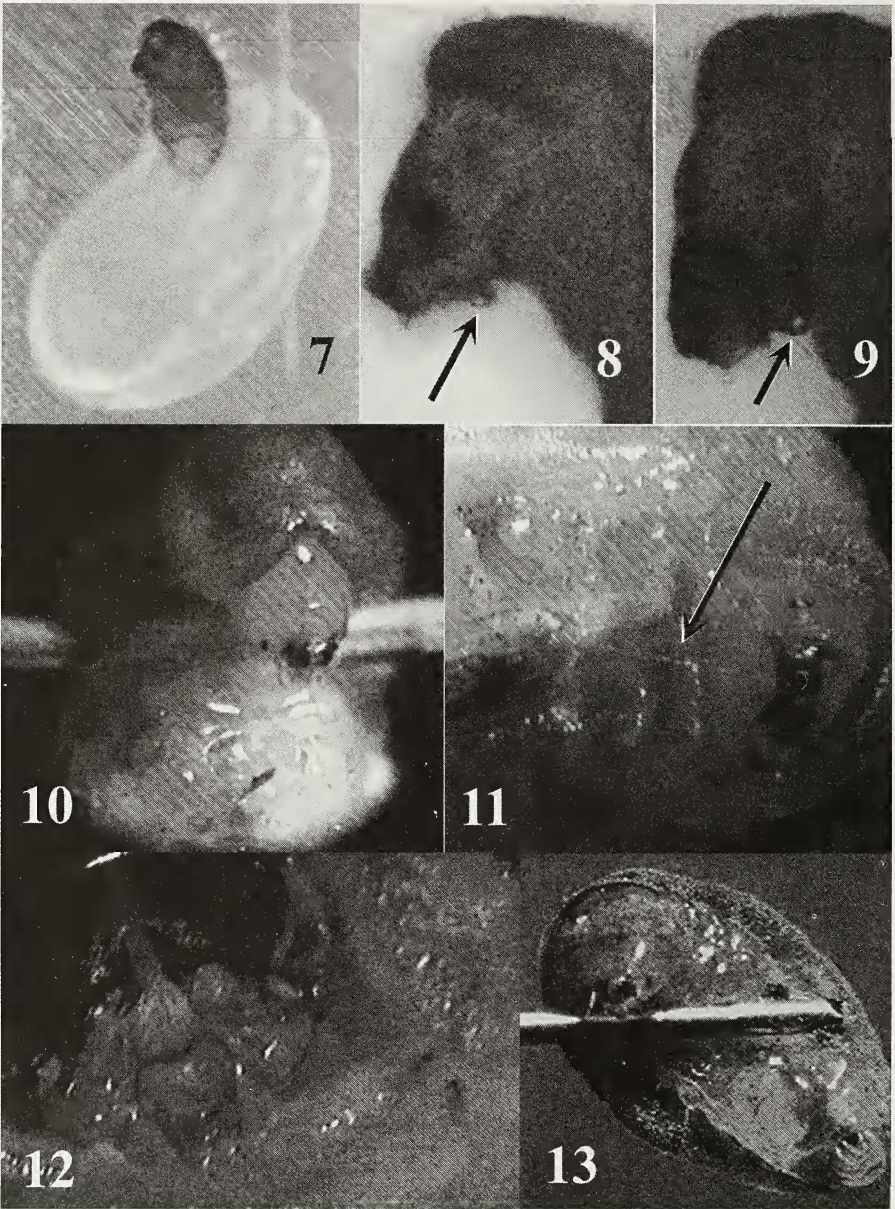


Figs. 4-6. Locomotion and ventral surface of larval Megalopygidae. 4-5: Late instar *Megalopyge basalis* (head on right end) (from 16 mm film by Kjell Sandved). 4) Clasping a wire with prolegs and thoracic legs; 5) Viewed through a horizontal piece of plexiglass; 6) Scanning electron micrograph of abdominal prolegs and subventral pads on A2 (top) to A3 of *Mesoscia pusilla* (scale bar = 0.5 mm).

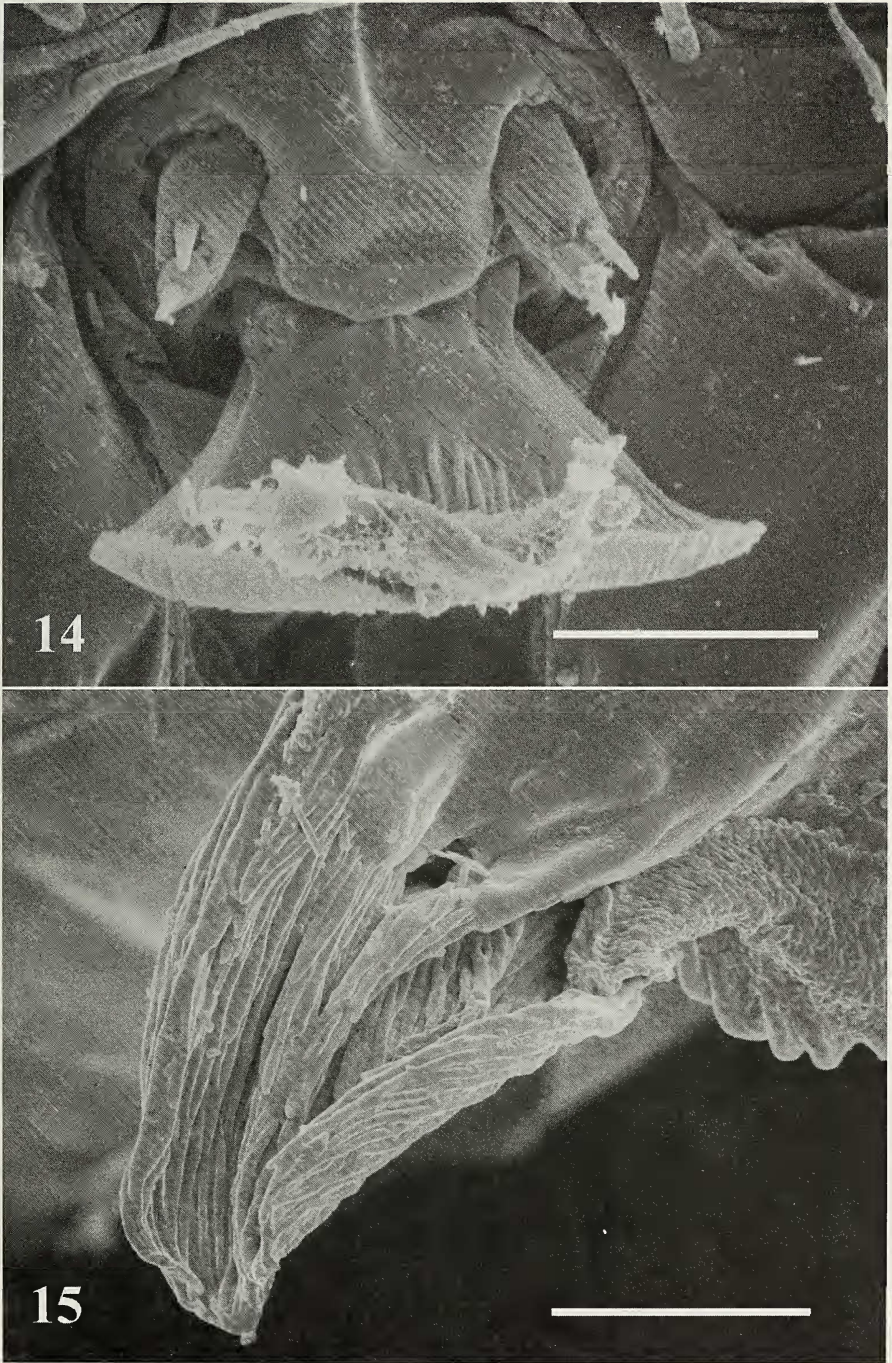
surfaces, as in species of megalopygids and caterpillars in other families (Epstein 1995).

Limacodidae. 1) *narrow surfaces*: Larvae ventrally grasp leaf edges, stems, or narrow vines along the midline (Figs. 11, 19), or from anterior to posterior (Fig. 10); anal prolegs do not grasp. Sticky silk can also help proximal abdominal segments stick together while wrapping around a stem. Reduced thoracic legs have tactile function, while the pretarsal claw assists in grasping a leaf or petiole or in clutching silk applied to the posterior ventrum. 2) *flat surfaces*: The locomotory surface, which consists of a highly flexible cuticle with fungiform tactile setae, moves in fluid waves that expand laterally along the leading edge, progressively retracting from the substrate (Figs. 16, 17). Tactile lateral setae, located between the margins of the ventral surface and the spiracles, contact the substrate during locomotion. Waves can move in oblique angles when the larva shifts its head and thorax to either side. Larvae readily reverse motion either in straight or oblique waves. The vestigial anal prolegs, spinulose with less elastic cuticle, are raised off the substrate during locomotion. This assists in expelling frass while in motion or while feeding. 3) *silk*: Semifluid silk, or a fluid along with the silk, is laid down in figure-8 fashion by the spinneret on substrates during or prior to locomotion. The fluid can spread from the thoracic region to the 9th abdominal segment and aids in the adhesion of the suckers. The silk is also applied directly to the anterior ventrum by rearing up the head or to the entire ventrum on narrow surfaces when clasping from anterior to posterior. The apparently sticky silk strands on the ventrum help the suckers grip to flat or narrow substrates (Fig. 10). Unlike megalopygids, aidids and numerous other lepidopterans, the larvae often do not leave discrete strands of silk behind until the onset of cocoon construction. 4) *feeding and resting*: Larvae have heads retracted beneath the prothorax while the ventrum is laterally expanded and is suckered down to the substrate (assisted by surface film) (Fig. 18). When the ventral surface gets dirty, larvae will raise their anterior off the substrate and brush the thorax and first few abdominal segments with their spinneret from side to side.

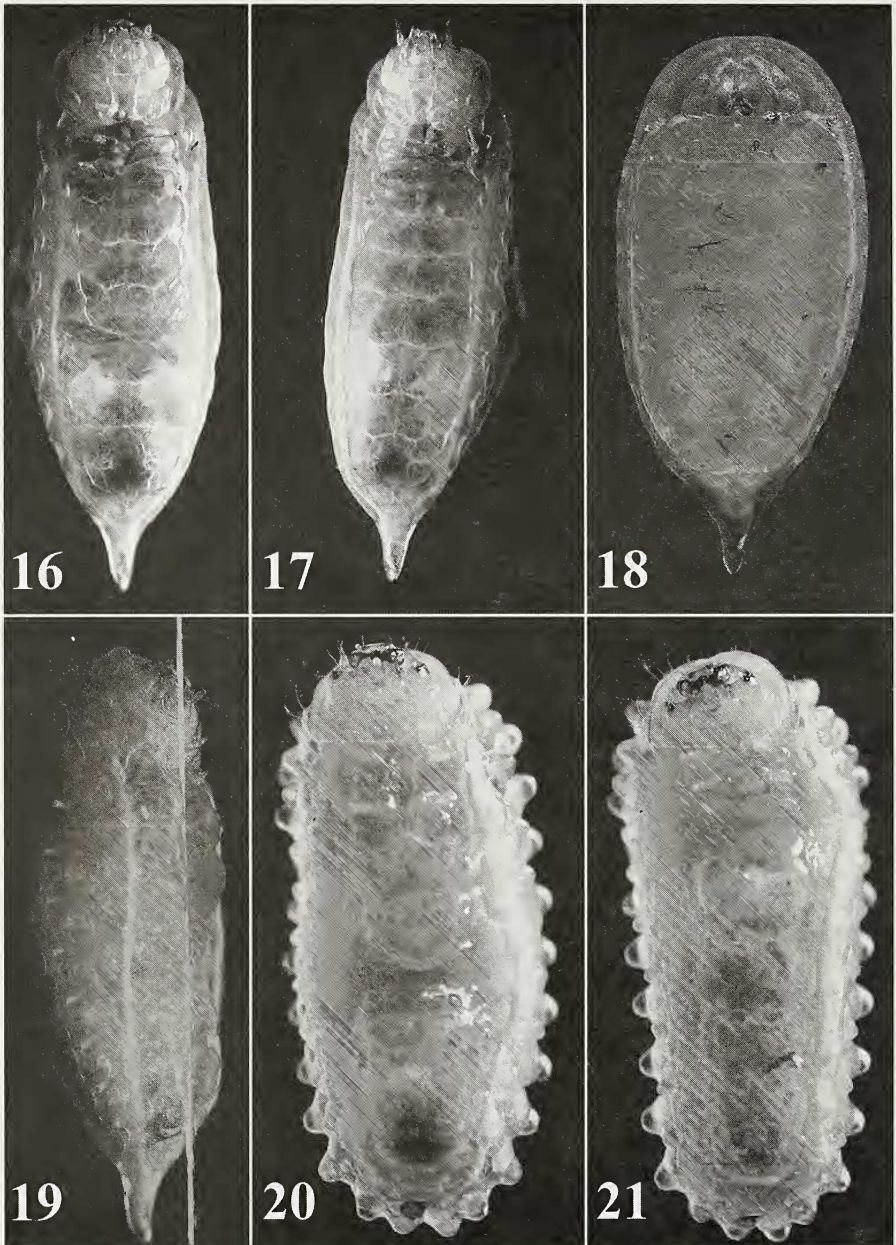
Discussion: The tight adhesion of the ventrum to the substrate, during locomotion or at rest, requires only small amounts of the liquid silk to provide surface tension. Use of scanning electron microscopy revealed no pores for fluid secretion on the ventral and lateral surfaces (Epstein 1996), as suggested by Holloway (1986). The presence of a liquid silk droplet was observed in *Prolimacodes badia* during egg eclosion (Figs. 7-9), although not during this stage in other species (e.g., *Isa textula*, *Tortricidia pallida*). The



Figs. 7–13. Use of semifluid silk in larval Limacodidae (from 8 mm video). 7) Egg eclosion of *Prolimacodes badia*; 8, 9) Detail of silk droplet on end of spinneret during egg eclosion of *P. badia* (arrows point to droplet); 10) Late instar larva of *Tortricidia pallida* claspng stem from anterior to posterior while applying silk to posteroventral segments; 11) Silk strand of *T. pallida* at the end of a twig (arrow points to silk strand) (note medial claspng of ventral surface on the left); 12) Detail of spinneret and ventral thorax of late instar *P. badia* (viewed through clear plastic from above); 13) Late instar *T. pallida* obliquely grasping stem while applying fluid silk to it.



Figs. 14-15. Spinnerets of first and last instar Limacodidae in related genera *Prolimacodes* and *Semyra* (scale bar length in parentheses). 14) First instar *Prolimacodes badia* with silk debris on distal margin (50 μ m); 15) Last instar *Semyra coarctata* complex (27 μ m).



Figs. 16–21. Locomotion in larval Limacodidae and Dalceridae (viewed from above through glass). 16–19: *Semyra coarctata* complex (photos by Chip Clark). 16) Near middle of locomotion sequence; 17) At the end of a locomotion sequence; 18) Larva at rest with ventrum laterally expanded and head retracted; 19) Lateroventral view of larva medially clasping the edge of the glass. 20, 21: *Dalcerides ingenita* (photos by Laurie Minor-Penland). 20) Near middle of locomotion sequence; 21) At the end of a locomotion sequence.

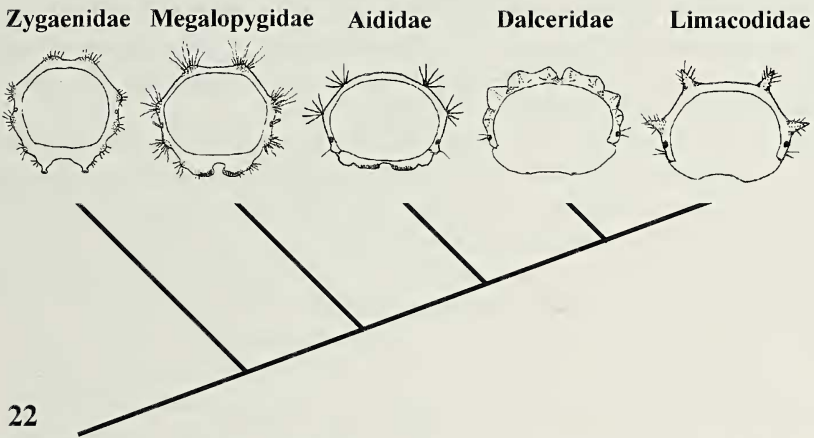


Fig. 22. Evolution of the ventral surface in the limacodid-group families viewed in cross section of proleg segment (after Epstein 1996).

spinneret, whether broad at the apex in early instars (Fig. 14) or narrow in late instars (Figs. 12, 15), functions similarly in both the use of the silk and in cleaning the ventral surface. Although the prolegs are highly reduced, their gripping of narrow substrates appears to be aided by a dense pad of ventral muscles revealed by dissection.

Dalceridae. Locomotion (Stehr & McFarland 1985; Figs. 20, 21) and spinneret function in dalcerid larvae are similar to those found in limacodids. Tactile lateral setae used to touch the substrate during locomotion are shifted dorsad, above or near the spiracles, compared to those in limacodids. This probably is due to the relative closeness of spiracles to the locomotory surface. Semifluid silk was observed in *Dalcerides ingenuita*, though not at egg eclosion. Reports of a “shiny path” trailing behind dalcerid larvae (Genty et al. 1978) may have been from broad ribbons of silk laid on the substrate or the result of cleaning with the spinnerets. Fluid debris has been observed following “brushing” on the anteroventral abdominal segments. Small crochets, present only in mid- to late instars (Stehr & McFarland 1985, Epstein 1996), appear not to have any function on smooth leaf surfaces. However, they may be used by the prepupa when crawling inside the diffuse cocoon.

EVOLUTION OF LOCOMOTION IN THE LIMACODID GROUP

The most noticeable trend when viewing locomotion of the limacodid group in phylogenetic sequence is the increased proportion of the ventral surface in direct contact with the substrate (Fig. 22). In megalopygids, at the base of the limacodid group, this is suggested by the shortness of prolegs relative to presumed zygaenid ancestors and the addition of prolegs on A2 and A7. Moving from megalopygids to aidids, contact increases as a result of the reduction of lateral and subventral verrucae to smooth warts. In the limacodid + dalcerid clade, further contact results from reduction

of the prolegs on A2–7 to suckers, formation of suckers on A1 and A8, and the flexibility to the ventral cuticle (Epstein 1996). The relatively large thoracic legs and grasping of narrow surfaces in Somabrachyidae, in addition to other plesiomorphies (Epstein 1996), suggest that this family may be a primitive lineage of the limacodid group.

The increased contact of the larval ventral surface suggests a specialization toward smoother host plants. Features of megalopygids that are effective in clinging to smooth surfaces include the membranous pads on the prolegs, and presumably, in some species, pads on subventral verrucae. The presence of smooth subventral and lateral warts in aidids, which contact the substrate during locomotion (versus setose verrucae), are also indicative of this type of host plant specialization. Absences of crochets on A2 and A7 proleg segments in many megalopygids and in aidids, apparently independent losses (Epstein 1996), are also suggestive of this trend. The smooth and flexible ventrum in the limacodid + dalcerid clade, in conjunction with the spinneret and silk, assists in sticking to smooth host plant surfaces (see further discussion below).

Species in the limacodid group are often polyphagous, with the ability to switch host plants even in later instars (Dyar 1905, 1909, Epstein 1995). Perhaps predator selection influenced evolution in this direction, since a combination of slow growth (found throughout the group) and increased foraging time in seeking a specific host plant could lead to heavy losses of larval populations from parasitoids and predators. Switching to other host plant species with similar smooth-leaf textures and suitable chemical make-ups would theoretically decrease foraging time.

Caterpillar adaptations to predators have been thought to relate to defenses, such as group feeding in spiny caterpillars or crypsis, with locomotion not playing a role (Casey 1991). The majority of caterpillars of the limacodid group employ these defenses against predators and parasitoids. However, in limacodids and dalcerids especially, ventral adhesion to the hostplant and locomotion are so closely linked that locomotion can indeed be considered an adaptive strategy to avoid predation. Species in the two families show a marked specialization for cryptic behavior in their ability to crawl beneath smooth plant surfaces. This is further enhanced by having less visible mouthparts at leaf edges due to retractile feeding beneath the thorax, as in other members of the limacodid group (Epstein 1996). These larvae may also be less easily detected by parasitoids from their less apparent silk trails, perhaps gaining in survival from cryptic silk-use what they lose in not having the ability to dangle on silk to reach new host plants.

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