Revision and Phylogeny of the Limacodid-Group Families, with Evolutionary Studies on Slug Caterpillars (Lepidoptera: Zygaenoidea)

MARC E. EPSTEIN

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY · NUMBER 582

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ABSTRACT

Epstein, Marc E. Revision and Phylogeny of the Limacodid-Group Families, with Evolutionary Studies on Slug Caterpillars (Lepidoptera: Zygaenoidea). *Smithsonian Contributions to Zoology*, number 582, 102 pages, 409 figures, 7 tables, 1996.—The limacodid group, composed of Limacodidae (+ Chrysopolomidae), Dalceridae, Megalopygidae, Aididae, and Somabrachyidae, is revised, and diagnoses, redescriptions, and keys to larval and adult stages are provided for each family. Comparative morphology and ontogeny of the larval stage are emphasized. Immature stages, including first instars, of a number of taxa are figured for the first time. New character data for adults and immatures are presented, including the presence of larval crochets on abdominal segments A2–A7 and A10 in species of Megalopygidae and Limacodidae. Computer-assisted phylogenetic analyses of limacodid-group families using separate character-data sets from adult and immature stages produces congruent cladograms of equal parsimony, with Zygaenidae selected as the outgroup. Megalopygidae (Megalopyginae + Trosiinae) is found to be the most basal family among the limacodid group, and Aididae, previously a subfamily of Megalopygidae, is the sister group to the Limacodidae + Dalceridae clade. Chrysopolomidae is placed as a subfamily of Limacodidae based on new character evidence from adult and immature stages. Relationships of Somabrachyidae, Epipyropidae, and Cyclotornidae also are discussed. Previous interpretations of character homologies for abdominal prolegs in the larvae are revised based on the phylogenetic analysis, resulting in a novel hypothesis concerning the evolutionary transformation from prolegs to a slug-like ventral surface. New representations of homology for larval body setae and for juxta and valva of male genitalia also are given. Behavioral observations of immatures and adults of species in the limacodid group are presented, along with a review of their biology.

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Dedication

This contribution is dedicated to the memories of my father, Joseph Samuel Epstein, and fellow lepidopterists F. Martin Brown and B. Adrienne Venables.

Revision and Phylogeny of the Limacodid-Group Families, with Evolutionary Studies on Slug Caterpillars (Lepidoptera: Zygaenoidea)

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Introduction

Limacodidae (= Eucleidae, Cochlidiidae) is the richest (~ 1000 species) and most widespread moth family among a monophyletic group of five families in the Zygaenoidea, which I term the "limacodid group." Distributed worldwide, although primarily in the tropics, the family Limacodidae is related to the New World limacodid-group families Dalceridae (84 spp.) (Miller, 1994), Aididae (= Aidinae, Megalopygidae, 6 spp.), and Megalopygidae (~ 230 spp.) (Hopp, 1934; Becker, 1995). Two Old World relatives are Chrysopolomidae (35 spp.) and Somabrachyidae (~ 10 spp.). Restricted to Africa and Madagascar (Hering, 1937), Chrysopolomidae is placed herein as a subfamily of Limacodidae. The Somabrachyidae, often regarded as constituting a subfamily of Megalopygidae, are found in Africa and in Mediterranean Europe (Geertsema, pers. comm.; Freina and Witt, 1990).

The limacodid group is characterized by extemal-feeding larvae that have retractile heads and either prolegs on abdominal segments A2–A7 or a flexible, slug-like ventral surface. There is a wide diversity of larval forms in the limacodid group (Figures 1–6), although it is best known for spiny larvae that cause dermatitis. The Limacodidae, Megalopygidae, and Dalceridae are economic pests of palms and other plantation crops in the tropics (Genty et al., 1978; Cock et al., 1987).

Relationships among families in the limacodid group and their allies are poorly understood. In large part this is due to an incomplete knowledge of immature stages. Furthermore, there has been little detailed morphological study of immature stages or of adults.

Fortunately the fog is lifting. During the past decade there have been studies on the limacodid-group families Limacodidae (Holloway, 1986; Holloway et al., 1987; Epstein, 1988) and Dalceridae (Stehr and McFarland, 1987; Miller, 1994) as well as on others associated with them, such as parasitic families Epipyropidae and Cyclotomidae (Davis, 1987; Common, 1990); however, comparative morphology from these studies has been needed in order to gain a better understanding of the interfamilial relationships. I base my phylogenetic (= cladistic) analysis of the limacodid group on the comparative morphological data given herein and in other recent studies cited above. Although I do not treat characters of the Zygaenidae extensively, I examine them in phylogenetic context of the limacodid group.

Dyar (1895a, 1899b) believed ventral suckers in limacodid larvae to be derived from fusion of the membranous pads found in megalopygids. Hinton (1955:516), however, indicated that there was no convincing explanation for the "loss of abdominal prolegs" in Limacodidae. I introduce an alternative evolutionary hypothesis to explain the formation of suckers on the ventral surface of limacodids. This hypothesis is based on

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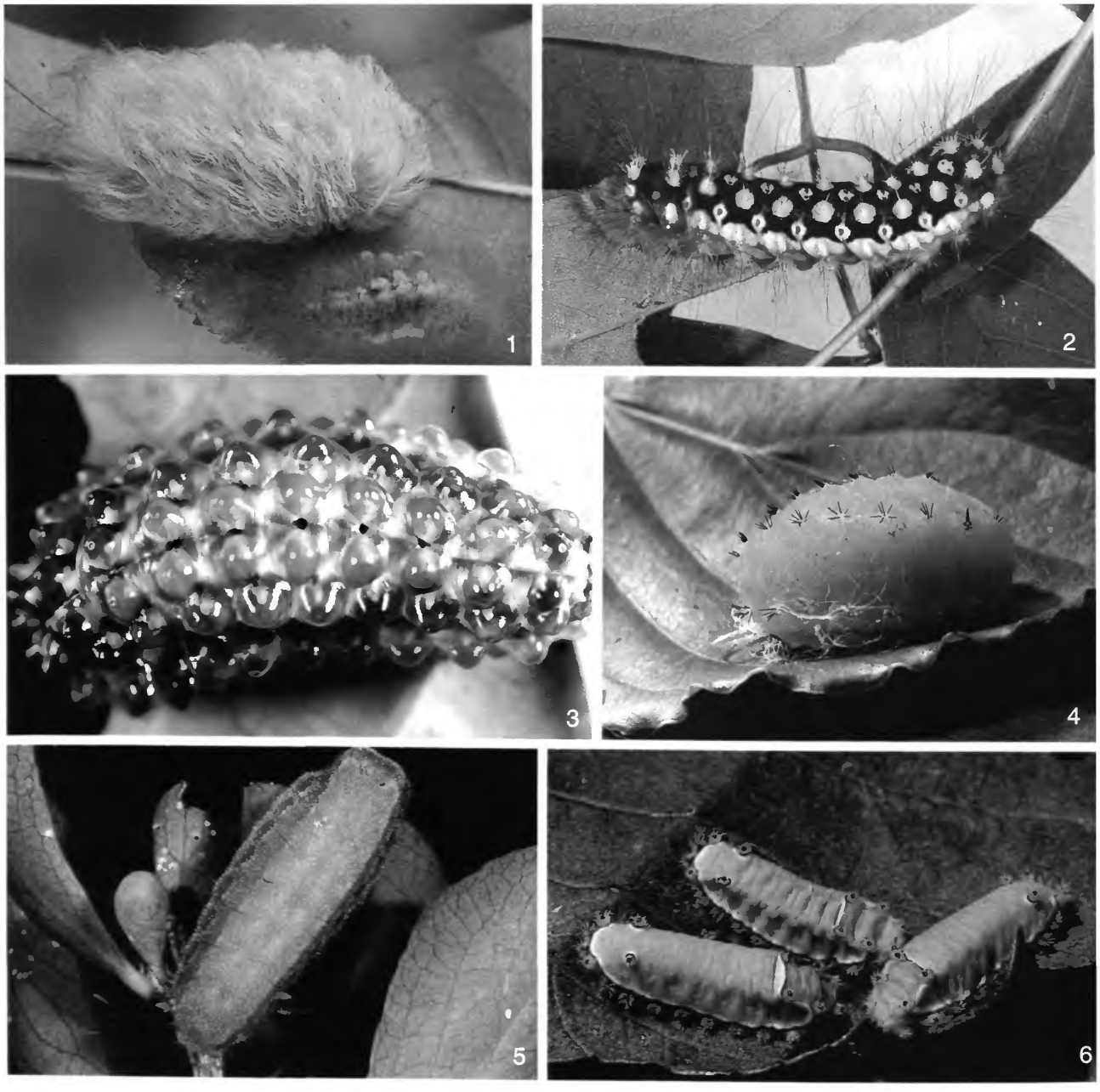

FIGURES 1–6.—Habitus of live larvae (late instars) in the limacodid group: 1, two species of *Megalopyge* (Megalopyginae), Pakitza, Peru (photo by K. Sandved); 2, *Norape cretata* (Trosiinae), USA, Maryland (photo by D. Ferguson); 3, *Dalcerides ingenita* (Dalceridae), USA, Arizona (photo by F.W. Stehr); 4, *Aidos amanda* (Aididae), Venezuela (photo by K. Sandved); 5, *Chrysopoloma similis* (Chrysopolominae), northern Transvaal, South Africa (photo by N. Duke); 6, *Acharia* sp. (Limacodidae), Venezuela (photo by K. Sandved).

evidence of homology and on the results of phylogenetic analysis of the limacodid group. Other character homologies that I reinterpret include the larval setae on the thorax and abdomen, and the juxta and valva of the male genitalia.

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MATERIAL AND METHODS

Specimens examined for this work are listed in Table 1, with additional limacodid material reported in Epstein (1988), Epstein and Miller (1990), and Epstein and Becker (1994). Standard dissection and wing clearing procedures for adult specimens were used (Clarke, 1941). Drawings were made with the assistance of a camera lucida. Specimens studied by scanning electron microscopy (SEM) were glued to a stub using water-soluble household glue and were sputter-coated with gold-paladium in the SEM Laboratory, Smithsonian Institution. Immature stages examined by SEM were stored in 70% ethanol, put through a dehydration series to absolute ethanol, and critical-point dried. Pupal and larval exuvia, usually stored dry, were removed from cocoons and glued to a round coverslip, which was then taped to the SEM stub. Dry larval exuvia sometimes were softened with trisodium phosphate, stored in 70% ethanol, and later critical-point dried. Micrographs were taken using Cambridge Stereoscan 100 and Hitachi 570 scanning electron microscopes. Observations of larval behavior (functional morphology) were assisted by the

TABLE 1.—Specimens examined by SEM or dissected for character data, comparative morphology, or ontogenetic information. Immature stages: e = egg, I = first instar, L = post-first instar, Lex = larval exuvia, P = pupa, Pex = pupal exuvia, C = cocoon. Adults: M = male genitalia, F = female genitalia, H = adult mouthparts (SEM), T = tarsi (SEM), WB = whole body. (Collection data is given in parentheses.)

ZYGAENIDAE
Harrisina americana (Guérin-Méneville): (USA: Virginia, USNM) L; (USNM) e
Harrisina metallica Stretch: (Dyar, USNM) L
Levuana iridescens Baker: (Fiji: Clarke, USNM) P
Zygaena trifolii (Esper): (USNM) L; (Naumann) I

EPIPYROPIDAE
Fulgoraecia exigua (Hy. Edwards): (USA: Maryland, Epstein, USNM) P

MEGALOPYGINAE
Megalopyge crispata (Packard): (USA: Maryland, Epstein, USNM) I, L, P
Megalopyge nr. *melaina*: (Peru: Epstein, USNM) L, P, Pex
Megalopyge lanata Stoll: (Ecuador: USNM) L; (Ecuador: CMNH) L, P; (Panama: USNM) F
Megalopyge sp.: (Venezuela: Epstein, USNM) WB, e, F
Podalia sp.: (Venezuela: Epstein, USNM) WB, M
Megalopyge sp. (Venezuela: BMNH) I

TROSIINAE
Mesocia pusilla (Stoll): (Colombia: Genty, USNM) L
Norape corporalis Major: (Venezuela: Epstein, USNM) WB, M

AIDIDAE
Aidos amanda Stoll: (Venezuela: Epstein, USNM) F, M, WB, e, L, C; (Brazil: USNM) F
Aidos sp.: (Venezuela: BMNH, 2 specimens) L
Aidos sp.: (Brazil: BMNH, 2 specimens) Lex, Pex, C
Aidos yamouna (Dognin): (Peru: Sanders, USNM) Pex
Brachycodilla carmen (Schaus): (Brazil: USNM) WB, M

SOMABRACHYIDAE
Psycharium sp.: (South Africa: USNM, 2 specimens) L
Psycharium sp.: (South Africa: Cape Province, Geertsema, 2 specimens) e, I
Somabrachys aegrotus Klug: (Morocco: CMNH) M
Somabrachys sp.: (Algeria: BMNH) L

DALCERIDAE
Acraga coa (Schaus): (Mexico: USNM) F
Acraga infusa complex: (Colombia: Genty, USNM) e, L, P
Dalcera abrasa H-S: (Venezuela: USNM) T
Dalcerides ingenita (Hy. Edwards): (USA: Arizona, McFarland) e, I, L, P, C
Dalcerina tijucana (Schaus): (Brazil: USNM) (e, L)
dalcerid sp.: (Ecuador: CMNH) I

LIMACODIDAE
Acharia (= *Sibine*) sp.: (Venezuela: Epstein, USNM) I, L, P, A
Apoda biguttata (Packard): I
Belippa horrida Walker: (Taiwan: Rawlins, CMNH, 88-229) I, F
Belippa laleana Moore: (China, USNM) L
Crothaema sp.: (South Africa: northern Transvaal, Duke, USNM) Lex, P, C
Crothaema sp.: (Malawi: Rawlins, CMNH, 88-636) I, F
Euclea delphinii (Boisduval): (USNM) H
Euprosterna sp.: (Venezuela: Epstein, USNM) I, L, P
Heuretes sp.: (Dominican Republic: Rawlins, CMNH) I
Monoleuca semifascia (Walker): (USNM) e; (USA: Florida, Habeck) P
Natada subpectinata Dyar: (Colombia: Genty, USNM) L
Pantoctaenia prasina (Butler): (Malawi: Rawlins, CMNH, 88-634) e, I, F
Pantoctaenia gemmans Felder: (Swaziland: Duke, USNM, 2 specimens) L
Parasa chloris (Moore): (USNM) H
Phobetron hipparchia (Cramer): (Venezuela: Epstein, USNM) I
Phobetron pithecium Abbott and Smith: (USA: Virginia, J. Burns, USNM) C, Pex; (USA: North Carolina, USNM) WB, M
Prolimacodes badia Hübner: (USA: Connecticut, Wagner, USNM) I
Semyra coarctata complex: (Venezuela: Epstein, USNM) e, I, L, P, M, F
Talima postica Walker: (Venezuela: Epstein, USNM) I, L, P

CHRYSOPOLOMINAE
Achrocerides theorini (Aurivillius): (Cameroon: USNM) F
Strigivenifera venata (Aurivillius) (Uganda: USNM) T
Chrysopoloma similis Aurivillius: (South Africa: northern Transvaal, Duke) Lex, Pex, C

use of 8 mm micro- and macrovideo and the use of a 16 mm movie camera fitted with a macro lens. Locomotion and silk-spinning behaviors were observed on a glass substrate and were video recorded from beneath by using an inverted compound microscope.

Larval chaetotaxy used herein largely follows Stehr (1987b) and Tremewan (1985). The examination of first instars was a major part of this study because few first instars have been figured since Dyar's contributions in the 1890s and in 1907, and all of his first instar specimens now are lost. Specimens were obtained from the eggs of females collected at lights in the field. Later instars were collected or reared using basic methods described by Dyar (1899a). First-instar limacodids in many genera are figured herein for the first time. These include African *Crothaema* and *Pantoctaenia* (Rawlins, CMNH); Neotropical *Semyra, Talima, Euprosterna, Phobetron hipparchia* (Epstein, USNM), and *Heuretes* (Rawlins, CMNH); and Asian *Belippa* (Rawlins, CMNH). Also figured for the first time are first instars and pupae of Dalceridae; male and female genitalia of Aididae; and larvae, pupae, and female genitalia of Chrysopolominae (sensu nova). Larval and pupal descriptions of *Chrysopoloma similis* are based on exuviae, photographs (Figure 5), and sketches, all provided by N. Duke.

ABBREVIATIONS

Following is a list of abbreviations used in the text and figures:

1A–3A	anal veins
A1–A10	abdominal segments
AA	anterior apophysis
AC	accessory cell
Aed	aedeagus
AG	accessory gland
An	antenna
AP	posterior apophysis
AS	axial seta
AT	anal tube
CB	corpus bursae
Cr	crochets
Crm	cremaster
CuA_{1-2}	anterior cubital veins

CuP	posterior cubital vein
Cx	coxa
D	dorsal group (setae or derivatves D1–D2)
DB	ductus bursae
DS	ductus seminalis
En	epicranial notch
Epm	mesepimeron
Fe	femur
FS	frass-flipping seta
FW	forewing
Ga	galea
Gn	gnathos
HW	hindwing
Jx	juxta
L	lateral group (setae or derivatives L1–L3)
Lbr	labrum
Lg	leg
LL	lateral lobe
LP	labial palpus
M_{1-3}	medial veins
Md	mandible
ML	mesal lobe
MSD	subdorsal proprioceptor group (setae or derivatives MSD1–MSD2)
MV	ventral proprioceptor seta
MT	Malpighian tubules
Mx	maxilla
MXD	proprioceptor seta
MxE	maxillary extension
MxP	maxillary palpus
OB	ostium bursae
Ov	oviduct
PA	papillae anales
Pl	proleg
PP	paraproct seta
R1	sensillum
R_{1-5}	radial veins
Rs	radial sector vein
S1–S2	stemmatal setae
Sa	saccus
Sc	subcostal vein
SD	subdorsal group (setae or derivatives SD1–SD3)
SG	sebaceous gland
Si	silk
SiP	silk pore
So	socius
Sp	spiracle
SpS	spiracular sensillum
Spt	spinneret
St	spermatheca
St1–St6	stemmata 1–6
Stm	stemmata
SV	subventral group (setae or derivatives SV1–SV4)
T1	prothorax
T2	mesothorax
T3	metathorax
Ta	tarsus
Te	tegumen
Ti	tibia
Tr	transtilla
Un	uncus
V	ventral group (seta or derivatives V1)
Va	valva
Vi	vinculum
XD	X-dorsal group (setae or derivatives XD1–XD2)

History of Classification of the Limacodid Group

This section focuses on the placement of the limacodid-group families within the classification of Lepidoptera from the 1890s to the present. Additional review of limacodid-group families, as well as of Epipyropidae and Cyclotornidae, is found under each family description below. Family-group names or groupings are given in the current sense. Names in the sense of the authors below are given in Table 2.

Packard (1894) believed the Megalopygidae to be generalized "bombycines," and he believed the Limacodidae to have "originated from the Saturniidae or forms allied to them" (Packard, 1893:83). During the same period, Dyar (1894) and Chapman (1893) placed Limacodidae, Megalopygidae, and Zygaenidae in "Microlepidoptera."

Epstein and Henson (1992) provide a historical review of Dyar's interests in both the Limacodidae and the higher classification of Lepidoptera. Dyar (1894), on the basis of larval setae, assigned Limacodidae, Megalopygidae, Zygaenidae (in part), and Procridinae (Zygaenidae) to "Anthrocerina." The Pterophoridae were temporarily added (Dyar, 1895a) but were later placed in uncertain status (Dyar, 1895b). Ultimately, Dyar combined the "Cossina" and Anthrocerina into the superfamily "Tineides" (Dyar, 1896a). Both Cossina and Tineides were known at the time as "Microlepidoptera."

Chapman (1893, 1894) lumped the Zygaenidae with Limacodidae and Micropterygidae into the pupa group "Incompletae." The two families Limacodidae and Micropterygidae were thought by Chapman (1894) to share homologous setal and proleg arrangements; however, these views did not gain acceptance (Dyar and Morton, 1895; Packard, 1895a:797; Hinton, 1955).

By 1895, Packard concurred with the idea of a close relationship between the Limacodidae and Megalopygidae, but he placed them below Tineina, apart from Zygaenidae (Packard, 1895a, 1895b). The Dalceridae were not included in these groupings because they were not recognized as separate from the Limacodidae or Megalopygidae until Dyar erected the family in 1898.

Fracker's (1915) Zygaenoidea included Chalcosiinae and Procridinae, Epipyropidae, Dalceridae, Megalopygidae, and

TABLE 2.—Family- and subfamily-group names of Zygaenoidea in the current sense and in the sense of the cited authors.

Author	Current sense	Old sense
Packard (1894)	Megalopygidae	Lagoidae
	Limacodidae	Cochliopodidae
Dyar (1894)	Limacodidae	Eucleidae
	Zygaenidae (in part)	Anthroceridae
	Procridinae (Zyg.)	Pyromorphidae
Chapman (1894)	Limacodidae	Cochliopodidae
	Micropterygidae	Eriocephalidae
Fracker (1915)	Limacodidae	Cochlidiidae
	Chalcosiinae (Zyg.)	Chalcodidae
	Procridinae (Zyg.)	Pyromorphidae

Limacodidae. This classification has been expanded by modern workers to include all of the current subfamilies of Zygaenidae, Cyclotornidae, Somabrachyidae, Chrysopolomidae, and Heterogynidae (Common, 1975, 1990; Kuznetsov and Stekol'nikov, 1981; Minet, 1986; Scoble, 1992).

Except Zygaenidae, Brock (1971) placed most families previously in Zygaenoidea in the Cossoidea, based primarily on character systems of the adult thorax and forewings. Brock shifted Epipyropidae and Heterogynidae to Tineoidea.

Heppner (1984) retained Megalopygidae, Somabrachyidae, and Heterogynidae in Zygaenoidea, but he placed Epipyropidae, Cyclotornidae, and the remainder of the limacodid group in the Cossoidea. He did not provide justification, however, for this arrangement.

Brock's Cossoidea, except for the position of Epipyropidae and Heterogynidae, has been followed in recent catalogs (e.g., Fletcher and Nye, 1982) and geographic checklists and has been followed by the Zoological Record (Zoological Society of London, 1992–1993). It has been criticized, however, both for the weakness of its adult characters and because of the strength of immature-stage characters as evidence for Zygaenoidea in the earlier sense (Common, 1975; Kuznetsov and Stekol'nikov, 1981; Minet, 1986). For example, Kuznetsov and Stekol'nikov (1981) suggested that the musculature of the male genitalia does not provide any evidence of synapomorphies between the Cossidae and the limacodid group, and Minet (1986) provided a list of zygaenoid synapomorphies based mostly on immature stages.

Currently, even Brock no longer subscribes to the arrangement in his earlier work. He included the "Eucleoidea" and Zygaenoidea in the Zygaeniformia, apart from the Cossiformia (Brock, 1990). I follow herein the superfamily grouping of Common (1990) and Minet (1986).

Biology

The biology of the Limacodidae was reviewed by Holloway (1986) and by Cock et al. (1987), both of whom emphasized the Old World literature. Either host plant records or natural enemies of Neotropical members of the limacodid group were given by Lima (1945), Silva et al. (1968), Biezanko et al. (1974), Miller (1994; Dalceridae only), and Epstein (1995; Aididae only).

LARVAE.—Limacodid-group larvae are frequently polyphagous and feed on old or tough leaves, as illustrated by larvae of temperate species that feed on oaks from July through September (Dyar, 1899a:241) when tannins and secondary compounds are at peak concentrations (Feeny, 1970). Larvae of limacodids and dalcerids reportedly feed on smooth leaves of trees and shrubs (Dyar, 1899a; Miller, 1994). In early instar larvae of the limacodid group, leaf feeding is characterized by the consumption of mesophyll from one surface (Figure 9). Not until the third or fourth instar do larvae feed on the entire leaf. Middle to late instars feed with their heads retracted beneath the thorax, while clasping the leaf edge by using flaps on each side of the prothorax (Figure 10). This probably makes it more difficult for a predator viewing the larva from below to detect the motion of mouthparts. Limacodid, dalcerid, and aidid larvae are further concealed by the absence of verrucae or urticating setae on the prothorax.

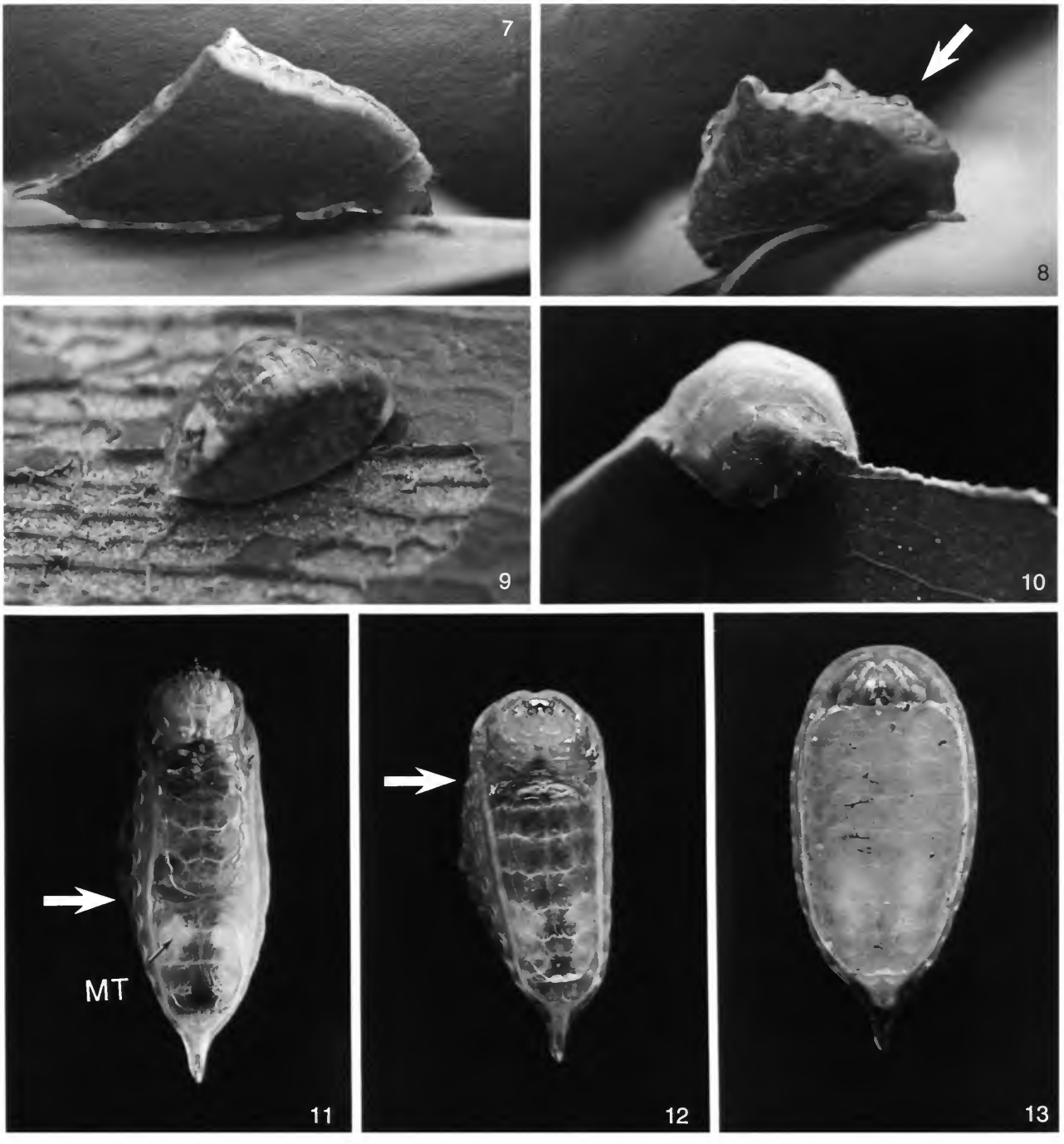
A general review of the medical literature on the urticating setae of Lepidoptera included those of limacodids and megalopygids (Delgado Quiroz, 1978). Pain-producing histamines have been reported in venomous setae of limacodid species and in a species of zygaenid (Itokawa et al., 1985). Megalopygid verrucae bear urticating setae as well as plumose setae. Long plumose setae have been considered to be merely ornamental (Figure 1) (El-Mallakh et al., 1986); however, these "harmless" setae spread the toxin released from the sharp spines beneath.

When disturbed, some smooth limacodid larvae secrete droplets from pores on the dorsum (Figure 8). This has been reported in *Prolimacodes badia* (as *Limacodes*, see Patton, 1891:43; as *Eulimacodes*, see Dyar, 1896a:173, 177), and it occurs in the related *Semyra coarctata* complex (Figure 8). Although their chemistry is unknown, the droplets often smell like the host plant (Patton, 1891).

Larvae of the Dalceridae have gelatin-covered setae. This sticky coating has been shown to be a deterrent to ants, and it is regenerated following removal (Epstein et al., 1994). The production and chemistry of this integumental coating is presently under study in collaboration with T. Eisner and S. Smedley (Cornell University).

Unique aspects of locomotion in caterpillars of the limacodid group can be observed laterally or from below as a larva crawls on glass (Figures 11, 12). The ventral abdominal segments in limacodids and dalcerids move in fluid waves, or peristalsis. This is facilitated by the extreme flexibility of the ventral cuticle, reduction in proleg size, and by having additional segments in complete contact with the substrate (e.g., segments A1–A2, A7–A9). The presence of suckers, in varying degrees of development, on abdominal segments A1–A8 also may increase the adhesion of the ventrum. Capable of forward or reverse locomotion, a forward wave begins when the venter of abdominal segment A9 contacts the substrate, because the A10 proleg is raised during locomotion. As a wave progresses, the portion retracted from the substrate is followed by a lateral bulge until it reaches the first abdominal segment. When a larva angles its head and thorax to turn, an oblique wave follows. On narrow surfaces, such as leaf edges and stems, larvae can clasp longitudinally from each side of the venter or can clasp from anterior to posterior.

Hinton (1955:516) suggested that in limacodid larvae "a liquid is secreted over the [ventral] cuticle." In limacodid and dalcerid caterpillars, I find that the liquid, at least in part, is semifluid silk. The apparently sticky silk is dabbed on the substrate, sometimes in a figure eight, with the brush-like spinneret (Figures 152–156, 158–162). Although the production of a thin ribbon of silk by *Apoda limacodes* Hufnagel (as *Limacodes testudo*) was reported by Chapman (1894), semi-



FIGURES 7–13.—Larval biology in *Semyra coarctata* complex (Limacodidae) (7, 8, 10–13, photos by C. Clark): 7, lateral view; 8, "defensive" droplets secreted on the dorsum (arrow); 9, early instar feeding; 10, late instar feeding on leaf edge (note mouthparts covered by prothorax); 11–13, ventral surface viewed from below, through glass (note Malpighian tubules); 11, 12, during locomotion (arrow points to leading edge of wave); 13, resting prior to molt (note opaque ventrum and spinneret tucked under flexible cuticle). (MT = Malpighian tubules.)

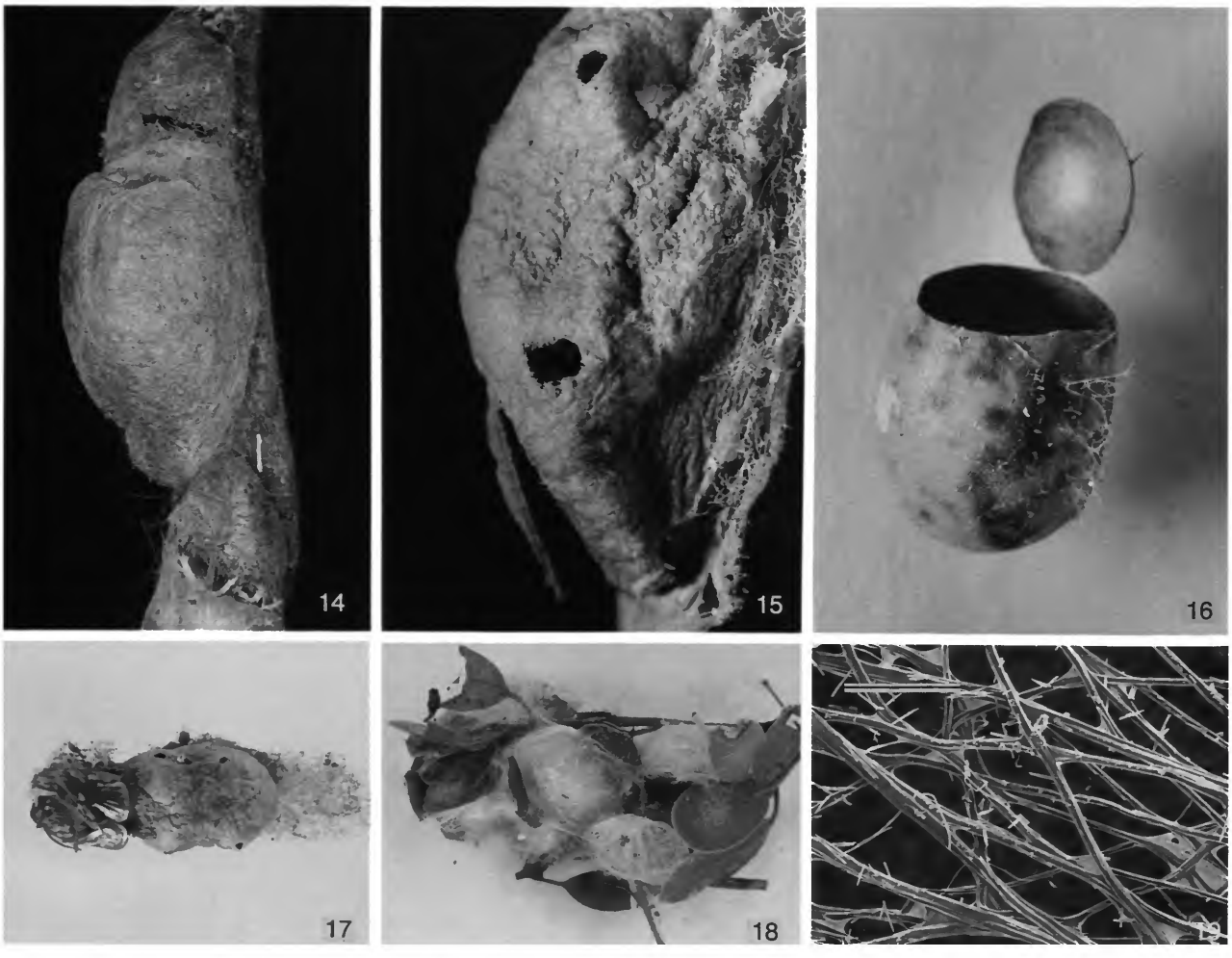
fluid silk has not been previously associated with the fluid on the ventral surface or with ventral surface stickiness. Using scanning electron microscopy I have found no secretory pores on the ventrum that could produce the fluid (Figures 265–270),

as was suggested by Holloway (1986:51). I also have observed that brush-like spinnerets in limacodids and in dalcerids (Figures 152–156) clean off debris that stick to the ventrum, enabling the caterpillars to adhere to substrates more efficiently.

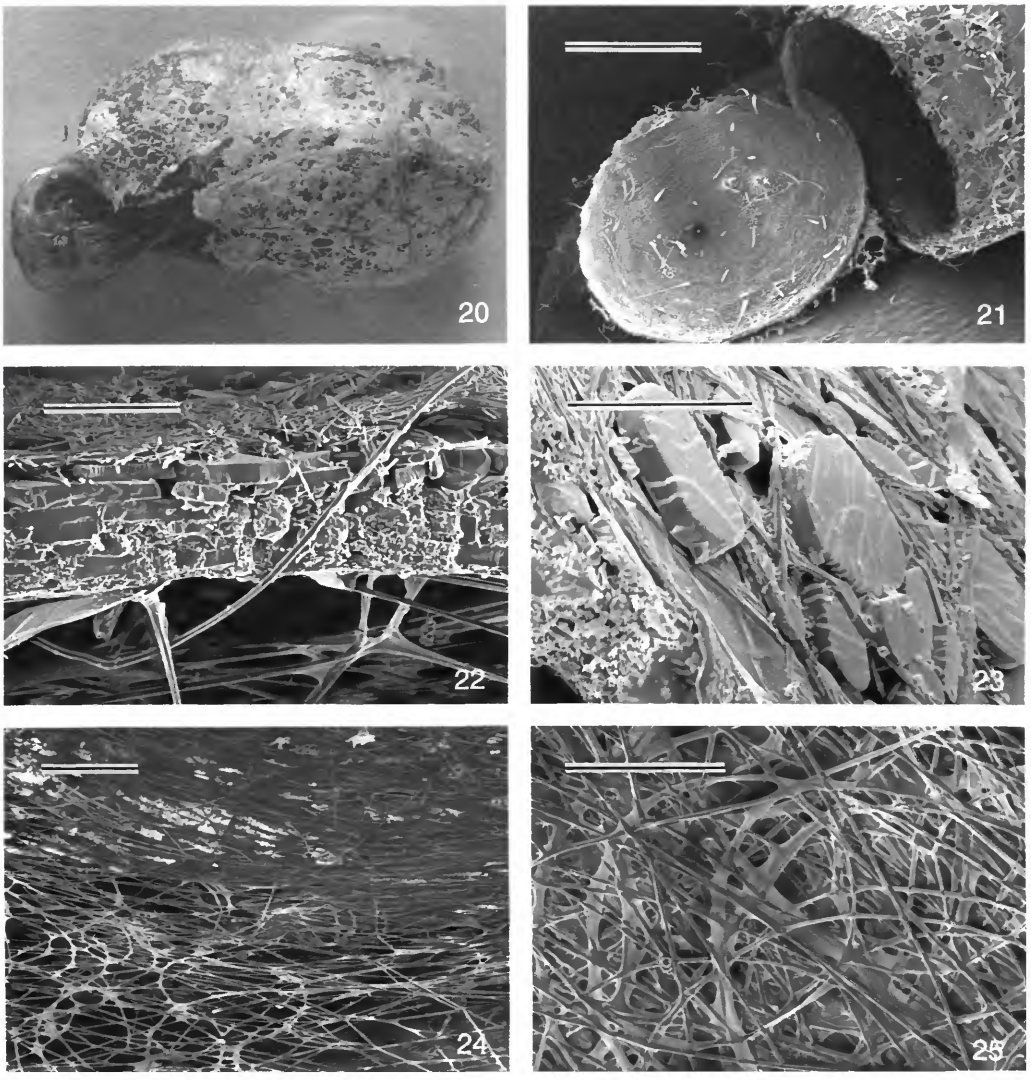
Locomotion in larval aidids (e.g., *Aidos amanda*) is similar to that in limacodids and dalcerids, except the ventrum is much less flexible (pers. obs.). The motion of the megalopygid ventrum on smooth surfaces is less fluid than it is in limacodids, dalcerids, or aidids because the membranous pads on the prolegs, rather than the entire ventrum, contact the substrate (Figures 252–257) (pers. obs.; Dyar, 1899b). The presence of these pads appears to be unique in the limacodid group.

Aidids, megalopygids, and somabrachyids (e.g., *Psycharium*) all issue normal silk when set on glass substrates (pers. obs.).

COCOONS.—The onset of cocoon construction in limacodid-group species is marked by final frass pellets that are frequently a chalky white. The release of fluid from pores on the dorsum of the prepupae helps to mat setae for a more compact shape; simultaneously, it reduces the size of the prepupa (to nearly one-half in limacodids (McNaulty, 1967)). A change in color and loss of pigment pattern also occur on the dorsum in limacodids (McNaulty, 1967) and dalcerids (e.g., *Dalcerides ingenita,* pers. obs.; F.W. Stehr, pers. comm.). The ventral cuticle in the two families becomes more opaque prior to molting or cocoon construction (Figure 13). Temperate species



FIGURES 14–19.—Cocoons of the limacodid group (14–16, photos by L. Minor-Penland; 17, 18, photos by V. Krantz): 14, *Megalopyge* nr. *melaina* (Megalopyginae), Peru; 15, *Aidos* sp. (Aididae), Brazil (trap-door exit below); 16, *Talima postica* (Limacodidae), Venezuela; 17, *Aidos* sp., Brazil; 18, *Dalcerides ingenita* (Dalceridae); 19, detail of dalcerid cocoon silk (photo by S.E. Miller).



FIGURES 20–25.—Cocoon of *Semyra coarctata* complex (Limacodidae) (scale length in parentheses): 20, cocoon with pupal exuvia (photo by C. Hansen); 21, cocoon and lid (2 mm); 22, cross section of cocoon where lid has been detached (50 µm); 23, dried excretion on outside of cocoon from Malpighian tubules (50 µm); 24, silk on inside of lid (200 µm); 25, silk inside cocoon (100 µm).

of limacodids and megalopygids diapause in the cocoon as prepupae during the winter (pers. obs.).

With the exception of the Dalceridae, cocoons in the limacodid group have trap-door exits (Figure 15) or lids (Figures 16, 21). Lids are opened by the pupa (Schremmer, 1990), which pushes nearly completely out of the cocoon prior to eclosion (Figures 17, 20) (further description is given in the pupal morphology section, below).

Megalopygid cocoons (Figure 14) vary in shape depending on the amount of plumose larval setae incorporated into the cocoon. Those with highly plumose larvae tend to be softer, with the trap-door hidden by the outer mesh of silk, whereas other megalopygids have a harder, more leathery cocoon.

Aidid cocoons are spun between leaves and have one or two pairs of small round holes in the cocoon wall (Figures 15, 17). These holes are in the outer mesh only and seem to mimic parasitoid exit holes (Hopp, 1930, 1934; Forbes, 1942:396; Epstein, 1995).

Spun between leaves, dalcerid cocoons (Figures 18, 19) have an outer portion of diffuse silk and an oval inner chamber. Gelatinous warts on the larva are sloughed off in the inner chamber during its construction (e.g., *Dalcerides ingenita*,

pers. obs.). The pupae extend out one side of the chamber just prior to eclosion (pers. obs.; Dyar, 1925).

Similar to those found in Zygaenidae, limacodid cocoons (Figures 16, 20) are usually harder and more ovoid than cocoons in the other families. The circular lid of the limacodid cocoon, unlike the trap door in Megalopygidae and Aididae cocoons, is not visible prior to eclosion. In fact, the prepupa does not construct a hatch with a preformed lid but, rather, spins a circular region of weakness at one end (pers. obs.; Dyar and Morton, 1895:150; Common, 1990). In some limacodid genera, prepupae spray a white muddy liquid, excreted by the Malpighian tubules, from the anus once the mesh of the cocoon is formed. The liquid is spread around by the ventral surface of the prepupa and later dries into crystaline structures on the outside of the cocoon (Figure 23), forming layers between the outside and the inner silk wall (Figure 22) (pers. obs.; Ishii et al., 1984). Ishii et al. (1984) found that cocoons in *Monema flavescens* Walker contain 35% ash, with calcium oxalate crystals from the Malpighian tubules predominant, and 34% protein, made up of dense silk mesh and other sclerotized proteins that they presumed to be from salivary secretions. Ishii et al. attributed the hardness of the cocoon to the proteins rather than to the ash; however, the hardness of cocoons of a limacodid in the *Semyra coarctata* complex (Figures 20–25) may be due more to ash, as indicated by the crystals both on the external surface and in the layers seen in cross section of the cocoon (Figures 22, 23).

Prepupae in some limacodid genera incorporate deciduous spines (e.g., *Acharia* (= *Sibine*)) or tubercles (e.g., *Phobetron*) into the cocoon.

ADULTS.—The biology of the adult stage in limacodid-group species is poorly known. Adults have a tentiform posture, with wings held below the dorsal plane of the body (Figures 26, 28–30). Dalcerids and limacodids often position their heavily pilose front and middle legs in front of the head (Figures 29, 32). Male Limacodidae exhibit several unusual postures (Figures 31–36), which apparently do not occur in other limacodid-group families. These postures may aid in crypsis and provide visual cues for mating, or they may be important in receiving or broadcasting pheromones. Some prop themselves up on their hindlegs and wings, with their bowed-out forelegs resting on their midlegs (*Semyra coarctata* complex) (pers. obs.) or with forelegs raised (*Perola* spp., Figures 31, 34) (K.B. Sandved, pers. comm.). Males of *Scopelodes* hang upside down in a similar posture, except the long labial palpi protrude rather than the forelegs (Figures 35, 36) (K.B. Sandved, pers. comm.). It also is common for male limacodids to curl the abdomen cephalad above their bodies (Figure 30).

Adult feeding in the limacodid group has not been reported until recently. In the laboratory, *Podalia bolivari* (Heylaerts) will feed on a solution of water and honey absorbed on cotton (Miller et al., 1995). I found that some limacodid species drink liquid in the laboratory: a female *Apoda biguttata* lowered its head into a sugar-water droplet containing 1% methylene blue; later dissected, it had a stained esophagus. Perhaps feeding occurs in most of the limacodid-group families, as galeae have been found in all families except Aididae and Somabrachyidae.

EGGS.—Within the limacodid group, only the Limacodidae are known to have scale-like eggs (i.e., dorsoventrally flattened), laid either individually or in overlapping clusters (Figures 39, 40). A few limacodid species cover their eggs with scales (e.g., *Monoleuca semifascia* and *Pseudonapaea trigona* (Turner)) (Dyar, 1914; N. McFarland, pers. comm.). Limacodid eggs are similar to those of some zygaenids, including *Lactura* (Peterson, 1967; Common, 1990) and *Zygaena* (Tremewan, 1985). Preliminary observations on the chorion in the *Semyra coarctata* complex (Limacodidae), however, suggest it is much thinner than reported for *Zygaena trifolii* (Zygaenidae) (Fehrenbach, 1995), an indication that its chorion is perhaps nonlamellar (J. Regier, pers. comm.). The eggs of the zygaenid *Harrisina americana* (Procridinae) are ovoid and are laid in nonoverlapping groups (Peterson, 1967), similar to those of megalopygids and dalcerids.

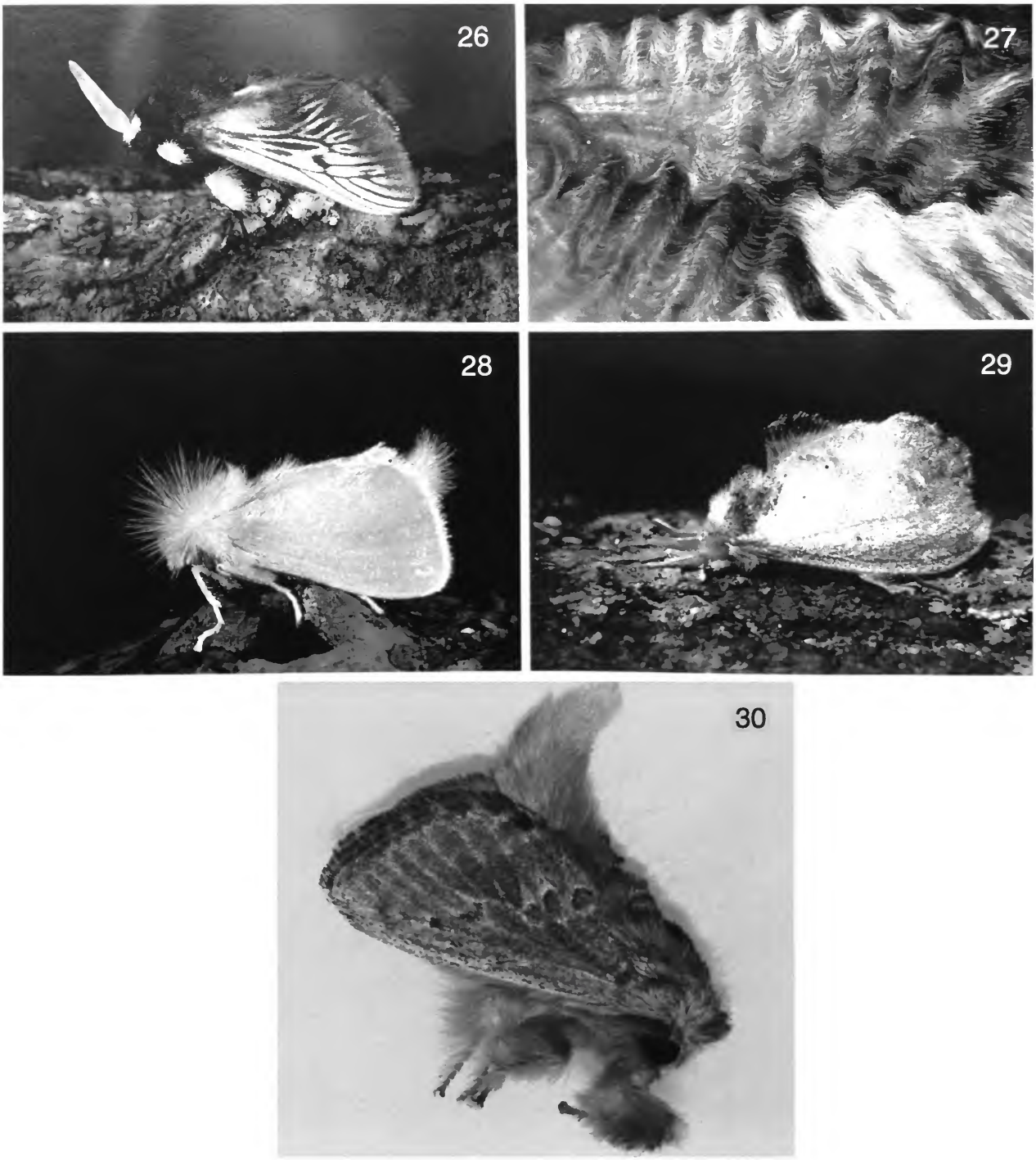
Megalopygid and dalcerid eggs are covered during oviposition. Megalopygid eggs are blanketed with piliform scales from a pouch on the end of the abdomen (Figure 37). Dalcerid eggs are coated with a fast-drying fluid secreted by accessory glands (Miller, 1993); a number of flattened scales from the female are attached (Figure 38).

Morphology

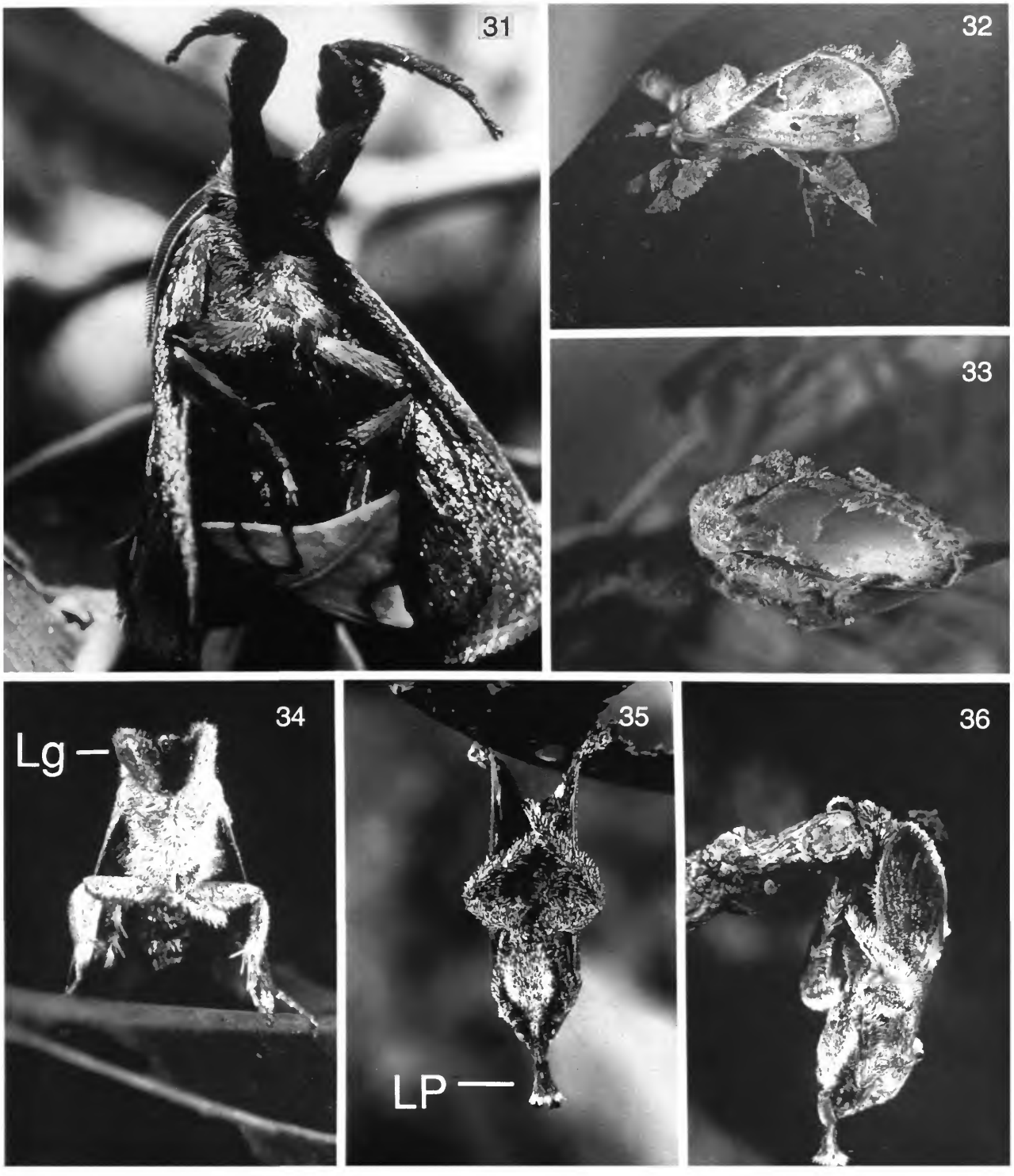
This section reviews the literature on the morphologies of adults and of immature stages in the limacodid-group families and contributes new findings as well. Comparative information on the families Zygaenidae, Epipyropidae, and Cyclotornidae is presented when it is pertinent to homology. New World limacodid generic complexes cited herein and their constituent genera are listed in Table 3.

TABLE 3.—New World limacodid generic complexes cited herein and their constituent genera. Nomenclature for Neotropical genera follows Becker and Epstein, 1995.

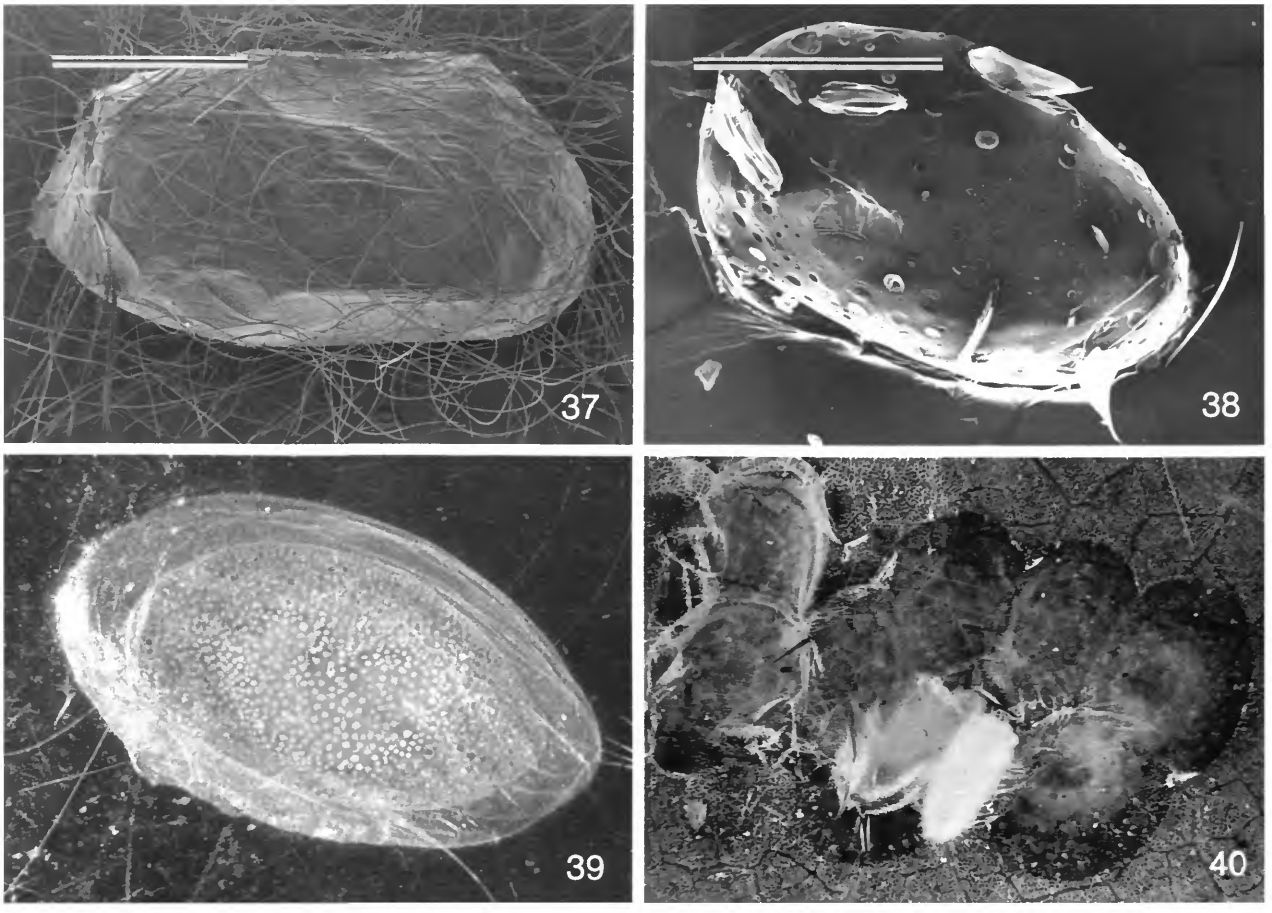
Generic complex	Genera included
Apoda	*Apoda, Heterogenea, Lithacodes, Packardia, Tortricidia*
Phobetron	*Alarodia, Euphobetron* (in part), *Heuretes, Isochaetes, Leucophobetron, Microphobetron, Phobetron, Vipsophobetron*
Prolimacodes	*Dichromapterix, Euphobetron* (in part), *Prolimacodes, Semyra, Tanadema, Venadicodia*
Perola	*Blazia, Epiperola, Paleophobetron, Perola*
Natada	*Euprosterna, Isa, Narosopsis, Natada, Platyprosterna*
Parasa	*Acharia* (= *Sibine*), *Adoneta, Euclea, Monoleuca, Paraclea, Parasa, Talima, Zaparasa*
Vipsania	*Pseudovipsania, Ulamia, Vispsania*
Miresa	*Miresa* (near *Parasa* and *Vipsania* complexes)
Unplaced	*Hepialopsis* (in *Phobetron* or *Prolimacodes* complex), *Cryptophobetron*



FIGURES 26–30.—Postures in adults (26–29, photos by K. Sandved): 26, *Megalopyge* sp. (Megalopyginae), Costa Rica; 27, closeup of forewing of *Megalopyge salebrosa* (Clemens), Mexico; 28, *Norape* sp. (Trosiinae), Colombia; 29, *Minacraga* nr. *disconitens* (Dalceridae), Venezuela (det. S.E. Miller); 30, *Pseudanapaea trigona* (Limacodidae), Australia (photo by N. McFarland).



FIGURES 31–36.—Postures in adult male Limacodidae (photos by K. Sandved): 31, *Perola* sp., Amazonas; 32, *Euclea distrahens* Dyar, Costa Rica; 33, *Euphobetron cypris* (Grote), Costa Rica; 34, *Perola* sp., Brazil, Belem; 35, 36, *Scopelodes* sp., New Guinea. (Lg = leg, LP = labial palpus.)



FIGURES 37–40.—Eggs (scale length in parentheses): 37, *Megalopyge* sp. (Megalopyginae), Venezuela (500 µm); 38, *Dalcerina tijucana* (Dalceridae), Brazil (500 µm); 39, *Pseudanapaea trigona*, Australia (Limacodidae) (photo by N. McFarland); 40, egg cluster of *Euclea delphinii* (Limacodidae), USA, Maryland.

ADULTS

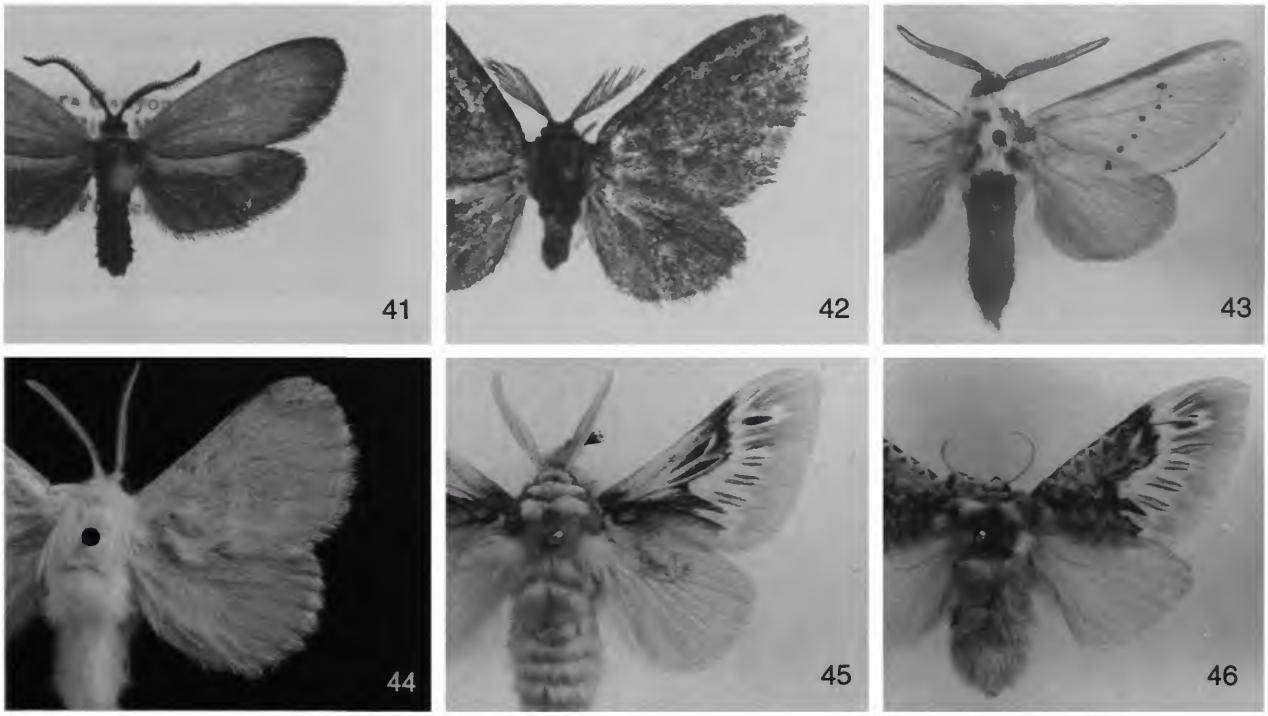
Members of the limacodid group are frequently woolly and have stout bodies and bipectinate male antennae (sometimes also bipectinate in females). They are small to medium large, with forewing lengths (base to apex) ranging from 4 mm to ~ 40 mm. This general habitus, along with the often spiny larvae, led early workers to place them in the "Bombyces."

The wings of limacodid-group species exhibit a diverse array of ground colors, including green (in limacodids), white, salmon, orange, reds, yellows, grey, and brown. Forewings in megalopygids (Figures 43, 45, 46), aidids (Figure 48), and limacodids (Figures 51, 52) commonly have distinct patterns, such as medial crescents or postmedial bands or spots. Dalcerids (Figure 49) tend to be less patterned, often having only vague "water marks." Hindwings in the group tend to be less distinctly patterned and may match or contrast the ground color of the forewings.

Sexual dimorphism of the wings also occurs. The most extreme cases are found in species that have smaller, partially clear-winged males. Examples include *Phobetron* species (Limacodidae) and *Podalia bolivari* (Megalopygidae) (Miller et al., 1995).

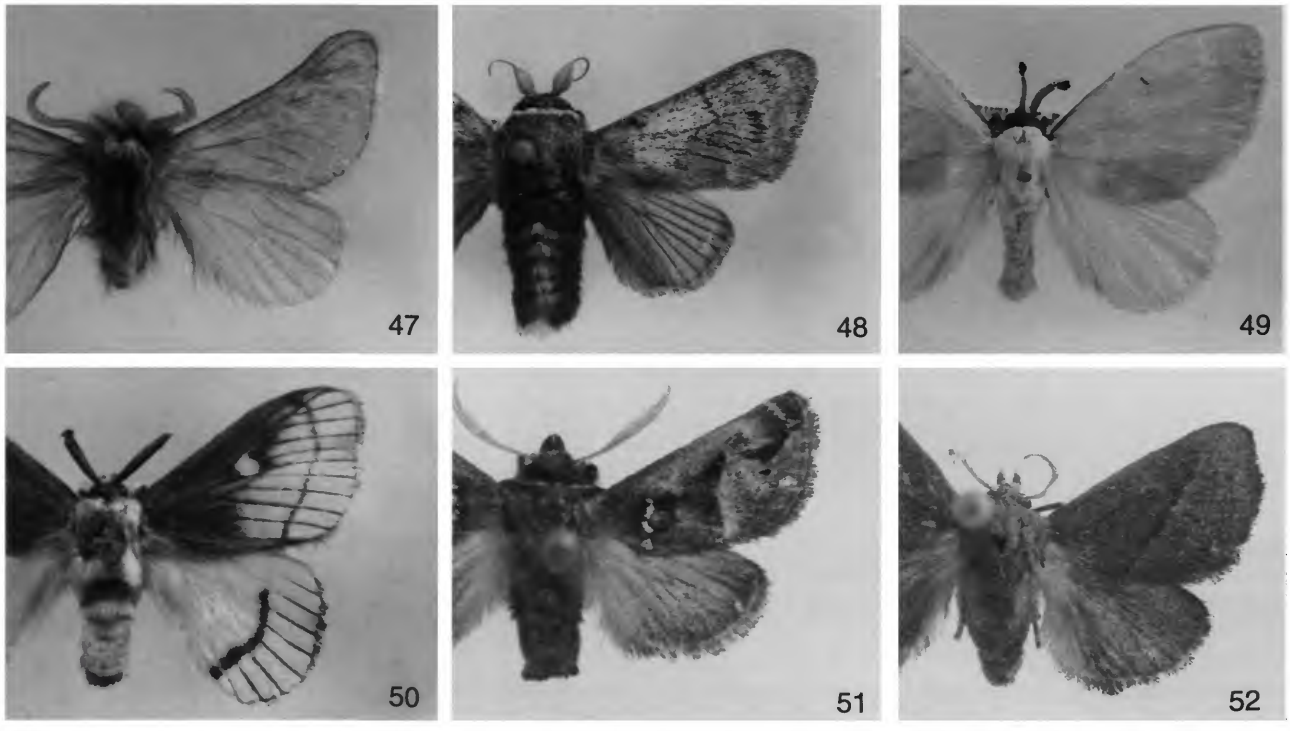
Scales on the wings and body range from piliform to dentate. Dentate scales are found in dalcerids (Miller, 1994) and limacodids. These are deeply divided in megalopygids (Khalaf, 1984), producing a woolly appearance (Figure 27). Spatulate scales occur in aidids (Dyar, 1895c).

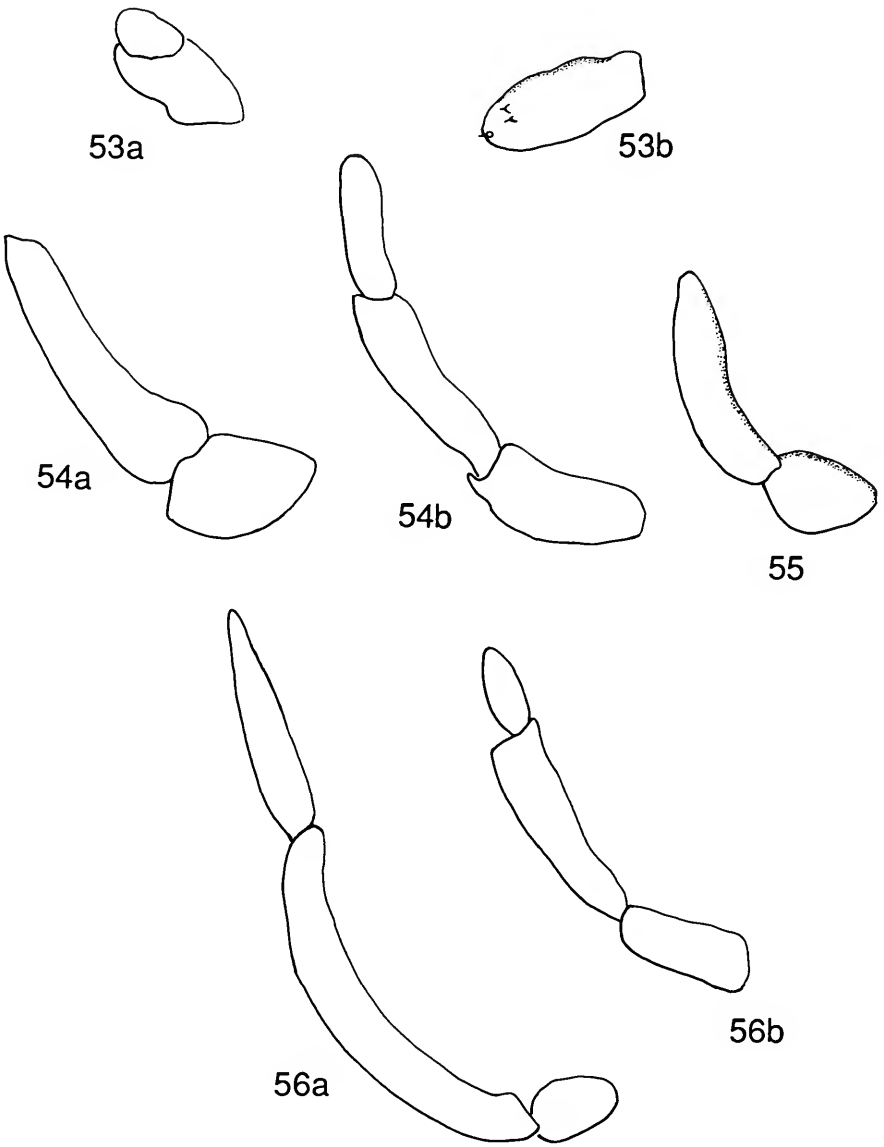
HEAD.—Although conspicuous ocelli are found in the Zygaenidae (Common, 1990), they are absent throughout the limacodid group. Jordan (1928) and Hopp (1934) described the presence of chaetosemata in the Megalopygidae and Aididae. In *Psycharium* (Somabrachyidae), the chaetosema forms "a belt extending from side to side," similar to that of *Anomoeotes* (Phaudinae, Zygaenidae) (Jordan, 1928:135). Chaetosemata are absent in the Limacodidae (Common, 1970), Dalceridae (Miller, 1994), Epipyropidae, and Cyclotornidae (Common, 1990).



FIGURES 41–46 (above).—Adult specimens of the limacodid group and other Zygaenoidea (male unless otherwise indicated) (photos by V. Krantz) (forewing length in parentheses): 41, *Pyromorpha dyari* (Jordan) (Zygaenidae), USA, Arizona (11 mm); 42, *Fulgoroides exigua* (Epipyropidae), USA, Maryland (5 mm); 43, *Trosia* sp. (Trosiinae) Colombia (19 mm); 44, *Norape cretata* (Trosiinae), USA, Maryland (13 mm); 45, 46, *Megalopyge salebrosa* (Megalopyginae), Mexico: 45, male (23 mm); 46, female (30 mm).

FIGURES 47–52 (below).—Adult specimens of the limacodid group (photos by V. Krantz) (forewing length in parentheses): 47, *Somabrachys* sp. (Somabrachyidae), Algeria (12 mm); 48, *Aidos amanda* (Aididae), Venezuela (17 mm); 49, *Dalcera abrasa* (Dalceridae), Venezuela (18 mm); 50, *Strigivenifera venata* (Chrysopolominae), Kenya (23 mm); 51, *Semyra coarctata* complex (Limacodidae), Venezuela (9 mm); 52, *Euprosterna elaea* (Druce) (Limacodidae), Venezuela (9 mm).



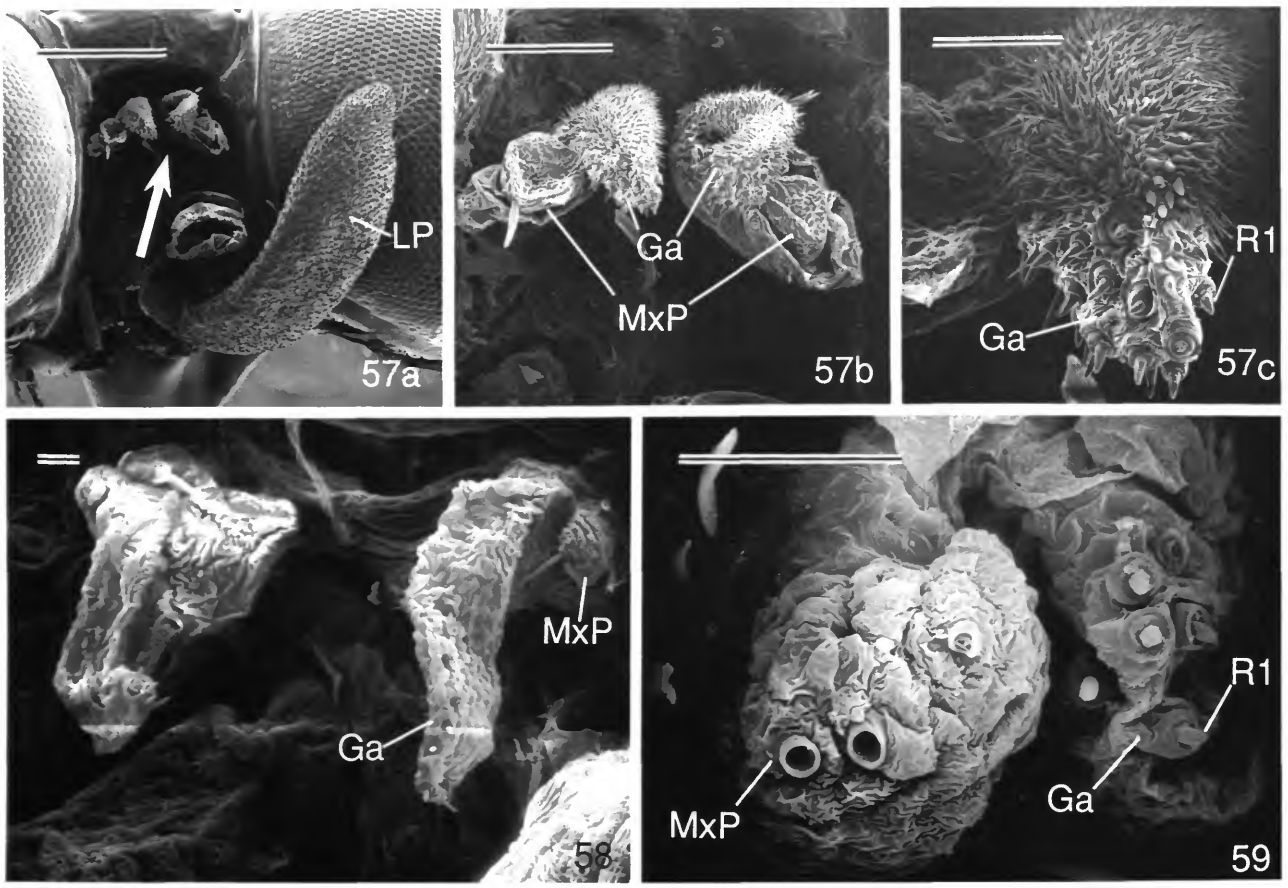


FIGURES 53–56.—Labial palpi (male unless otherwise indicated): 53*a*, *Norape corporalis* (Trosiinae), Venezuela; 53*b*, *Podalia* sp. (Megalopyginae), Venezuela; 54*a*, *Aidos amanda* (Aididae), Venezuela; 54*b*, *Brachycodilla carmen*, Brazil; 55, *Acraga coa* (Dalceridae), Mexico; 56*a*, *Vipsania rosabella* (Limacodidae) female, Costa Rica; 56*b*, *Phobetron pithecium* (Limacodidae), USA, North Carolina.

Clubbed male antennae, common in the Zygaenidae, do not occur in the limacodid group. Male antennae are bipectinate for their entire length in most of the Megalopygidae (except *Zyzypyge;* Hopp, 1934) (Figures 43–45), Somabrachyidae (Figure 47), and Dalceridae (Figure 49) but are bipectinate only in the basal two-thirds to one-third in Aididae (Figure 48). A complete range of these bipectinate conditions occurs in male Limacodidae (Janse, 1964), and there are unipectinate and filiform antennae as well.

Antennae are usually sexually dimorphic in the limacodid group, with pectinations being shorter or absent in the female (compare Figures 45, 46), although monomorphism can occur. Examples of broadly bipectinate antennae in both sexes include some species in the *Perola* complex (Limacodidae) and *Trosia* species (Megalopygidae). Species in the *Apoda* complex (Limacodidae) have filiform antennae in both males and females.

The labial palpus in the limacodid group varies in length and in the number of segments (Figures 53–56). It can be well developed in the Limacodidae, where it is usually three-



FIGURES 57–59.—Galeae (haustellum) and maxillary palpi in male Dalceridae and Limacodidae (scale length in parentheses). 57*a–c Dalcera abrasa* (Dalceridae) (courtesy of S.E. Miller): 57*a*, head, labial palpi, and location of galeae and maxillary palpi (arrow) (0.33 mm); 57*b*, galeae and maxillary palpi in *a* (see arrow) (120 µm); 57*c*, detail of galea and maxillary palpus in *a* (see arrow) (43 µm). 58, 59, galeae and maxillary palpus in Limacodidae: 58, *Parasa chloris* (30 µm); 59, *Euclea delphinii* (holes in maxilla are from missing scales) (30 µm). (Ga = galea, LP = labial palpus, MxP = maxillary palpus, R1 = sensillum.)

segmented (the second segment often more than twice the length of the other segments), upturned, and commonly reaching the vertex or beyond. The third segment, although frequently short (Figure 56*b*), is quite long in *Scopelodes* (Figures 35, 36) and *Vipsania* (Figure 56*a*). The Dalceridae lack segment three of the labial palpus (Figures 55, 57*a*) (Miller, 1994). The Megalopygidae can have two short segments (Figure 53*a*) (Philpott, 1926), as in Zygaenidae and Epipyropidae, or only one segment (Figure 53*b*). The Aididae, with either two or three segments (Figures 54*a,b*), generally have a longer labial palpus than do the Megalopygidae.

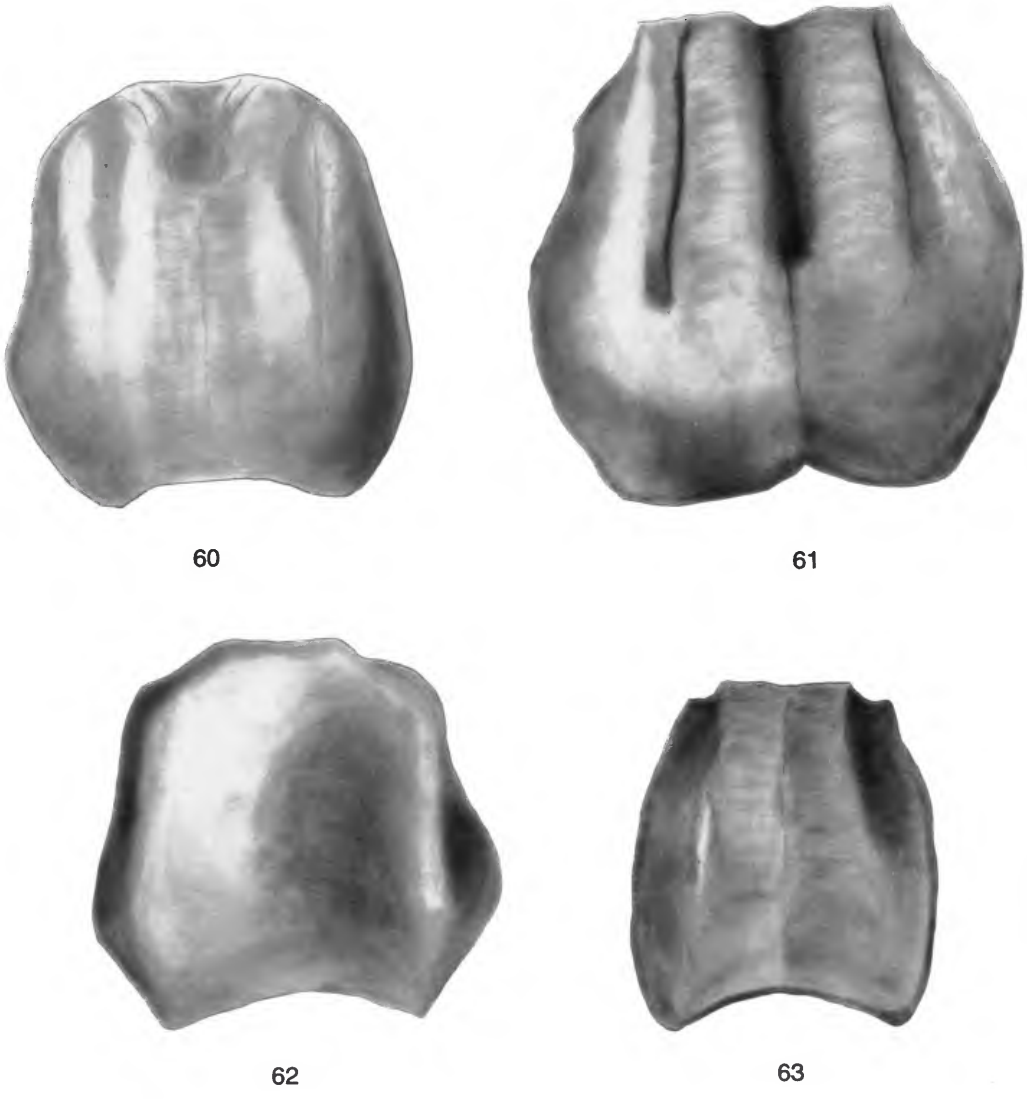
In contrast to the well-developed proboscis in the Zygaenidae, the galeae, or haustellum, in limacodid-group species are often vestigial or absent (Forbes, 1923; Common, 1990). In both the Limacodidae and Megalopygidae, galeae may be present or absent, sometimes within the same generic complex. Some of the Limacodidae have a narrow, coiled haustellum equal in length to the labial palpus, whereas in others the haustellum is the length of the first segment of the labial palpus (Figure 58) or shorter (Figure 59). Limacodid galeae are relatively smooth compared with those found in dalcerids, and they have R1 sensilla in the apical portion (sensilla homology follows Miller, 1991). Galeae of trosiine megalopygids (e.g., *Trosia, Mesocia*) are visible at low magnification of a dissecting microscope, whereas in megalopygines they are absent (e.g., *Megalopyge crispata*, see Philpott, 1926). Dalcerids have short galeae with dense spinules at the base (Figures 57*a–c*). The apical portion of the galea with R1

sensilla is incorrectly identified as the maxillary palpus by Miller (1994). Galeae are absent in aidids and somabrachyids.

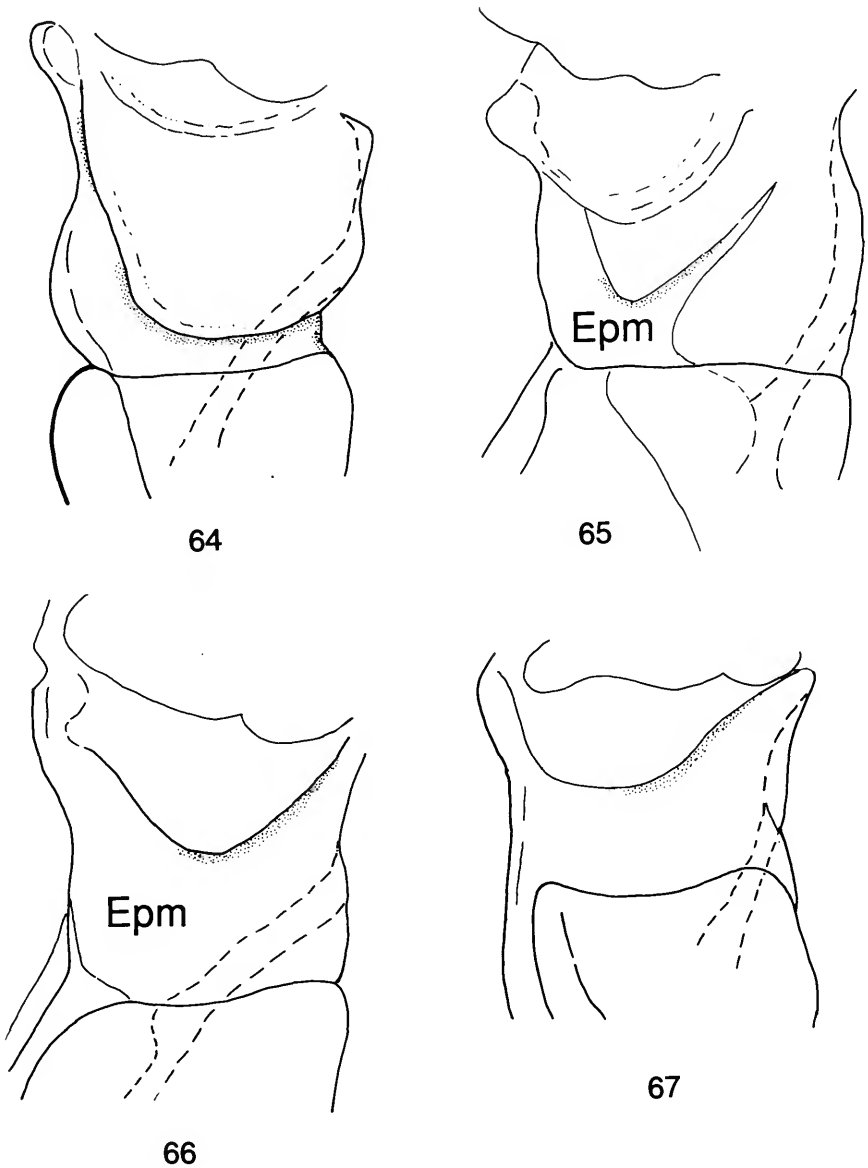
The Limacodidae can have a maxillary palpus of up to three segments (Philpott, 1926), although it also can be vestigial or absent. In *Euclea delphinii* the maxillary palpus is highly reduced rather than absent (Figure 59) (Epstein, 1988) as previously reported by Philpott (1926). In megalopygids it is either one segment and visible (e.g., *Trosia, Mesocia*) or absent (*M. crispata,* see Philpott, 1926). The maxillary palpus is vestigial in dalcerids (Figures 57*a-c*) (= galea in Miller, 1994) and is absent in aidids.

THORAX.—Hopp (1934:1071) reported a "deep longitudinal median fold" in the anterior portion of the mesonotum of Megalopygidae (+ Aididae), and Jordan (1928) noted additional lateral depressions (Figures 60, 61). Aidids have long medial and lateral depressions (Figure 61). Deep medial folds were also reported in the Zygaenidae (Jordan, 1928). These folds are not present in the Limacodidae or Dalceridae (Figures 62, 63), although carinate ridges in the former may be vestiges of lateral folds.

The degree of sclerotization of the mesepimeron appears to differ among families. The mesepimeron is more narrowly



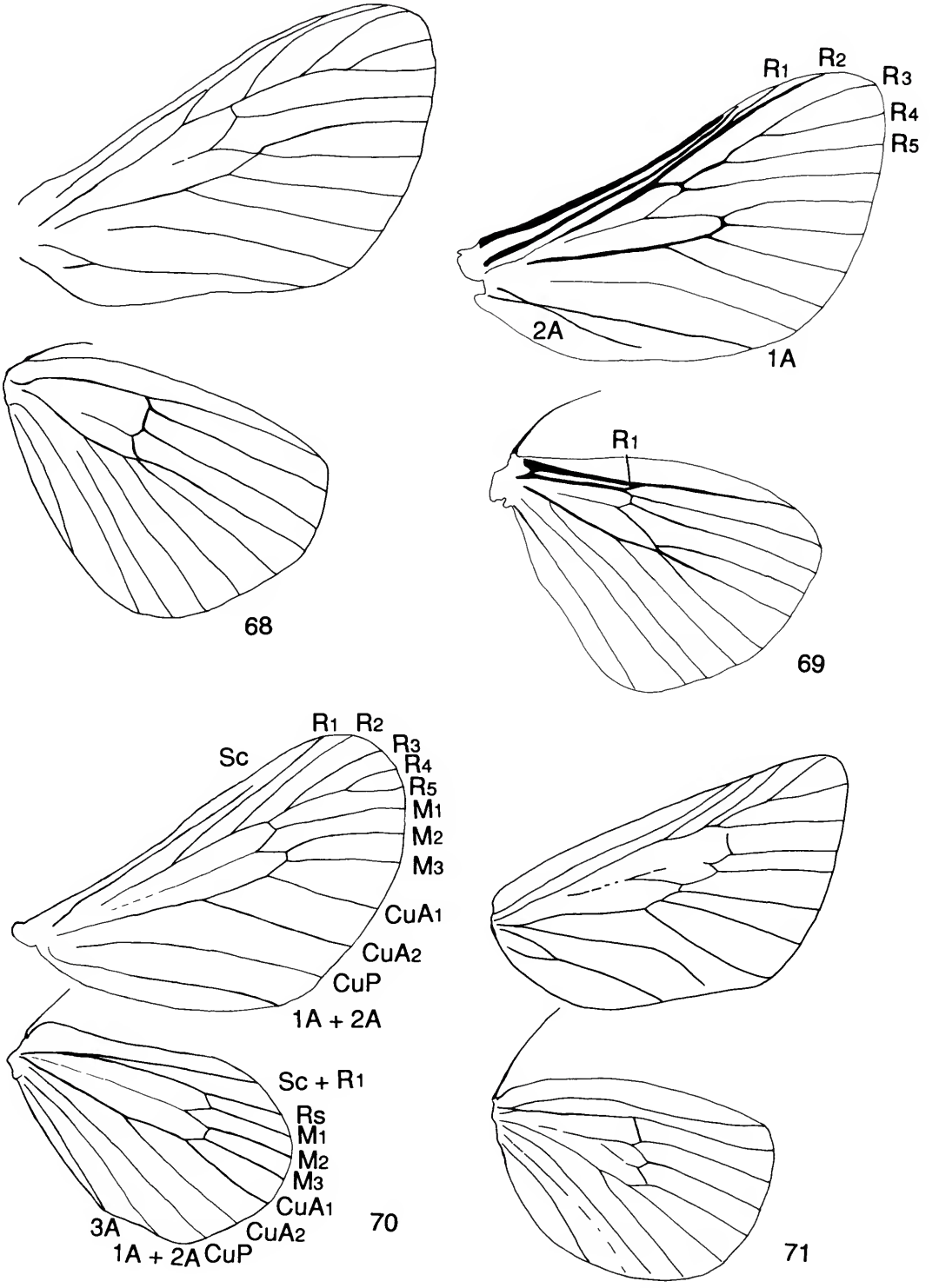
FIGURES 60-63.—Mesonotum in dorsal view: 60, *Podalia* sp. (Megalopyginae), Venezuela; 61, *Aidos amanda* (Aididae), Venezuela; 62, *Dalcerides ingenita* (Dalceridae), USA, Arizona; 63, *Acharia* sp. (Limacodidae), Venezuela.



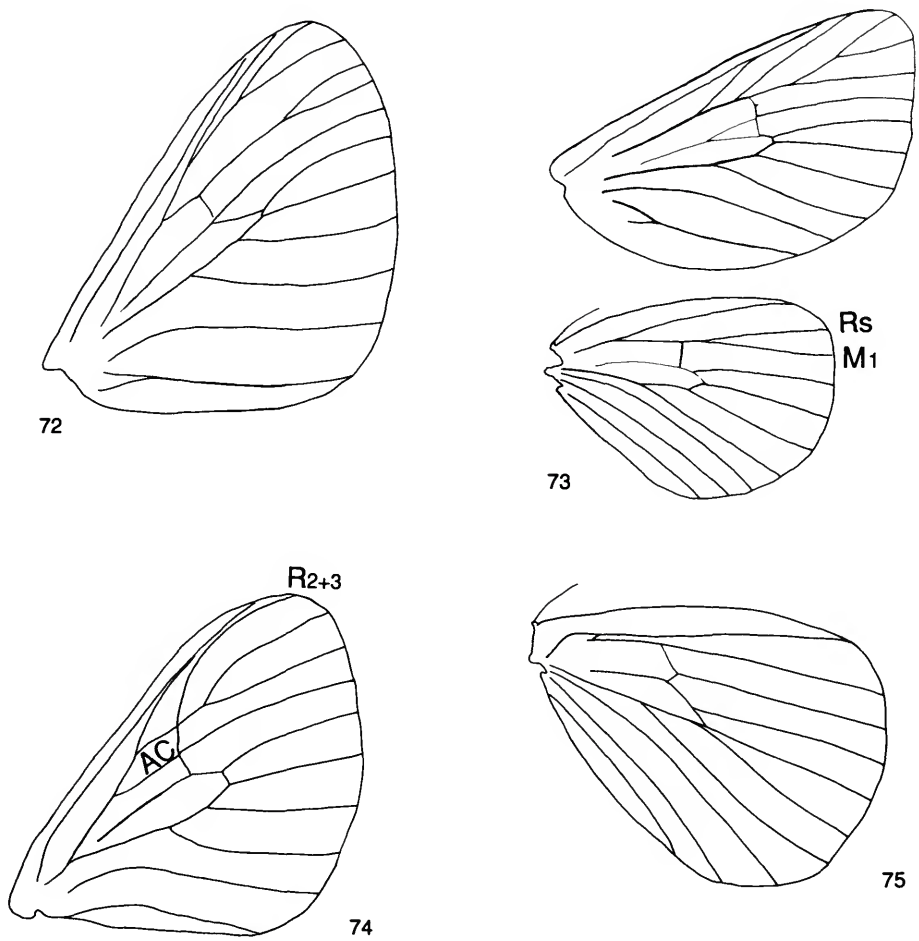
FIGURES 64–67.—Mesepimeron in lateral view, anterior to left: 64, *Phobetron pithecium* (Limacodidae); 65, *Acraga coa* (Dalceridae); 66, *Aidos amanda* (Aididae); 67, *Podalia* sp. (Megalopyginae). (Epm = mesepimeron.)

sclerotized in the Limacodidae and Dalceridae (Figures 64, 65) than it is in the Aididae and Megalopygidae (Figures 66, 67). Shepard (1930) noted similarities between the precoxal and pleural sutures in megalopygids and procridines (Zygaenidae). No tympanum is present in the Zygaenoidea.

Venation: Forewing R_{2-5} or R_{3-5} are usually stalked beyond the discal cell in members of the limacodid group. In contrast, those of zygaenids are usually not stalked or only one pair (e.g., R_3 and R_4) is stalked. Each limacodid-group family has a distinct forewing venation pattern. Both the Megalopygidae (Figures 68, 70) and Dalceridae (Figures 72, 74) have R_4 and R_5 stalked; the Dalceridae also have R_2 and R_3 stalked, although fusions can occur in either stalk (Figure 74) (Miller, 1994). The Aididae (Figure 69) and Limacodidae (Figures 71, 73) have R_3 stalked with R_4, although aidids are unique in having R_1 and R_2 stalked independently as well



FIGURES 68–71.—Wing venation: 68, *Norape corporalis* (Trosiinae), Venezuela; 69, *Brachycodilla carmen* (Aididae), Brazil; 70, *Podalia bolivari* (Megalopyginae); 71, *Pantoctaenia* (Limacodidae) (after Janse, 1964). (1A–3A = anal veins, CuA_{1-2} = anterior cubital veins, CuP = posterior cubital vein, M_{1-3} = medial veins, R_{1-5} = radial veins, Rs = radial sector vein, Sc = subcostal vein.)



FIGURES 72-75.—Wing venation: 72, forewing of *Minacraga disconitens* (Dalceridae), French Guiana; 73, *Acharia stimulea* (Clemens) (Limacodidae); 74, forewing of *Dalcerides sofia* (Dalceridae), Mexico; 75, hindwing of *Dalcerina tijucana* (Dalceridae), Brazil. (AC = accessory cell, M_1 = medial vein, R_{2-3} = radial veins, Rs = radial sector vein.)

(Figure 69) (Dyar, 1895). In addition, aidids and limacodids have R_3 and R_4 stalked off R_5, but the Limacodidae (+ Chrysopolomidae) may also have the two veins stalked off R_2 (or independent) or stalked between R_2 and R_5. Some limacodids have an R_5 that is split back from the radial sector and arises from the discal cell (Brock, 1971; Holloway, 1986). Jordan (1916:355) noted the presence of only four R (= Sc) in *Somabrachys* (Somabrachyidae).

Medial veins in the forewing discal cell can be either present or absent (Comstock, 1918). Jordan (1928) and Hopp (1934) reported their absence in Megalopygidae (+ Aididae); however, this is not always the case, as illustrated by *Norape* and *Podalia* (Figures 68, 70), and by *Brachycodilla* (Aididae) (Figure 69). The Dalceridae (Figure 74), Epipyropidae, Chrysopolominae (sensu nova) (Hering, 1937), and Zygaenidae (Common, 1990) sometimes have a radial vein (chorda) in the discal cell that forms an areole or accessory cell. Forewing anal veins are fused from near the base in the Dalceridae (1A + 2A) (Figure 72) (Miller, 1994) and Limacodidae (Figure 73). In the Aididae (Figure 69) and Megalopygidae (Comstock, 1893), 2A may diverge from 1A.

The frenulum occurs throughout the limacodid group, but it is lost in the Chrysopolominae (sensu nova) (Hering, 1937), three genera of Dalcerinae (Miller, 1994), and in some Megalopyginae (e.g., *Megalopyge basalis* (Walker)). Within Megalopyginae, the retinaculum is lost in *Megalopyge* (even in species that retain the frenulum) but is present in *Podalia* (Hopp, 1934).

Hindwing Sc + R_1 anastomoses with Rs for almost the entire length of the discal cell in the Trosiinae (Figure 68), female Megalopyginae (Hopp, 1934), Somabrachyidae (H. Geertsema, pers. comm.), and Zygaenidae (Jordan, 1928). Sc + R_1 is free from Rs or slightly fused near its base in the Aididae (Figure 69) (Dyar, 1895c), some Dalceridae (Figure 75) (Miller, 1994), male Megalopyginae (Figure 70), and Limacodidae (Figures 71, 73). In the limacodid-group families Dalceridae, Megalopygidae, Aididae, and in some Limacodidae (e.g., *Apoda* complex, *Pantoctaenia*) (Comstock, 1893), hindwing Rs and M_1 are separated by a perpendicular or oblique cross vein at the end of the discal cell (Figures 68–71, 75). Limacodidae is unique, however, in having Rs and M_1 stalked beyond the discal cell (Figure 73) in most of the genera.

Legs: The epiphysis on the foretibia is present in some of the Zygaenidae (e.g., Zygaeninae and *Lactura*) (Common, 1990), Heterogynidae (Scoble, 1992), and Somabrachyidae (e.g., *Somabrachys,* see Jordan, 1916; Hampson, 1920; Geertsema, pers. comm.) but is absent in the remainder of the limacodid group. The tibial spur formula for the Megalopygidae and Aididae is 0-2-2, whereas in Limacodidae and Zygaenidae it is either 0-2-2 or 0-2-4 (Janse, 1964; Common, 1990), and in Cyclotornidae it is 0-2-4 (Common, 1990). Tibial spurs are absent in the Dalceridae (Miller, 1994) and Epipyropidae (Common, 1990).

The fifth tarsomere is sexually dimorphic in most species of the limacodid group. There are dense clusters of sensilla trichodea on the ventral female tarsomere, usually with a concurrent reduction of scales (Figures 76–84); however, neither trait is found in males (Figures 87, 88). In female *Norape* (Trosiinae), the tarsomere has a narrow, medial group of scales with sensilla on each side (Figures 76, 77), whereas female *Megalopyge* have more medial scales (Figure 79). The tarsomere lacks scales among the sensilla in female aidids (Figure 82) and limacodids (+ Chrysopolomidae). Female dalcerids and some female limacodids (e.g., *Pantoctaenia* and *Crothaema*) have fewer sensilla, which are found in a narrow, distal band, and more numerous scales (Figures 85, 86, 91–95). Other Limacodidae have relatively short sensilla recessed in an ovate or quadrate pad, which is truncate on the distal end (Figures 96–103).

Female dalcerids have a large spur on each of the third through the fifth tarsomeres, of equivalent length to the surrounding scales (Figures 85, 89, 90).

ABDOMEN.—The Zygaenoidea have a tortricid-type sternum II (Kyrki, 1983). Spinose tergites have been reported in the Megalopygidae (+ Aidinae) (Hopp, 1934) and in *Boisduvalodes*. The latter was recently placed in Limacodidae (Viette, 1980); however, it shares a number of potential adult apomorphies with the Somabrachyidae (Geertsema, pers. comm.).

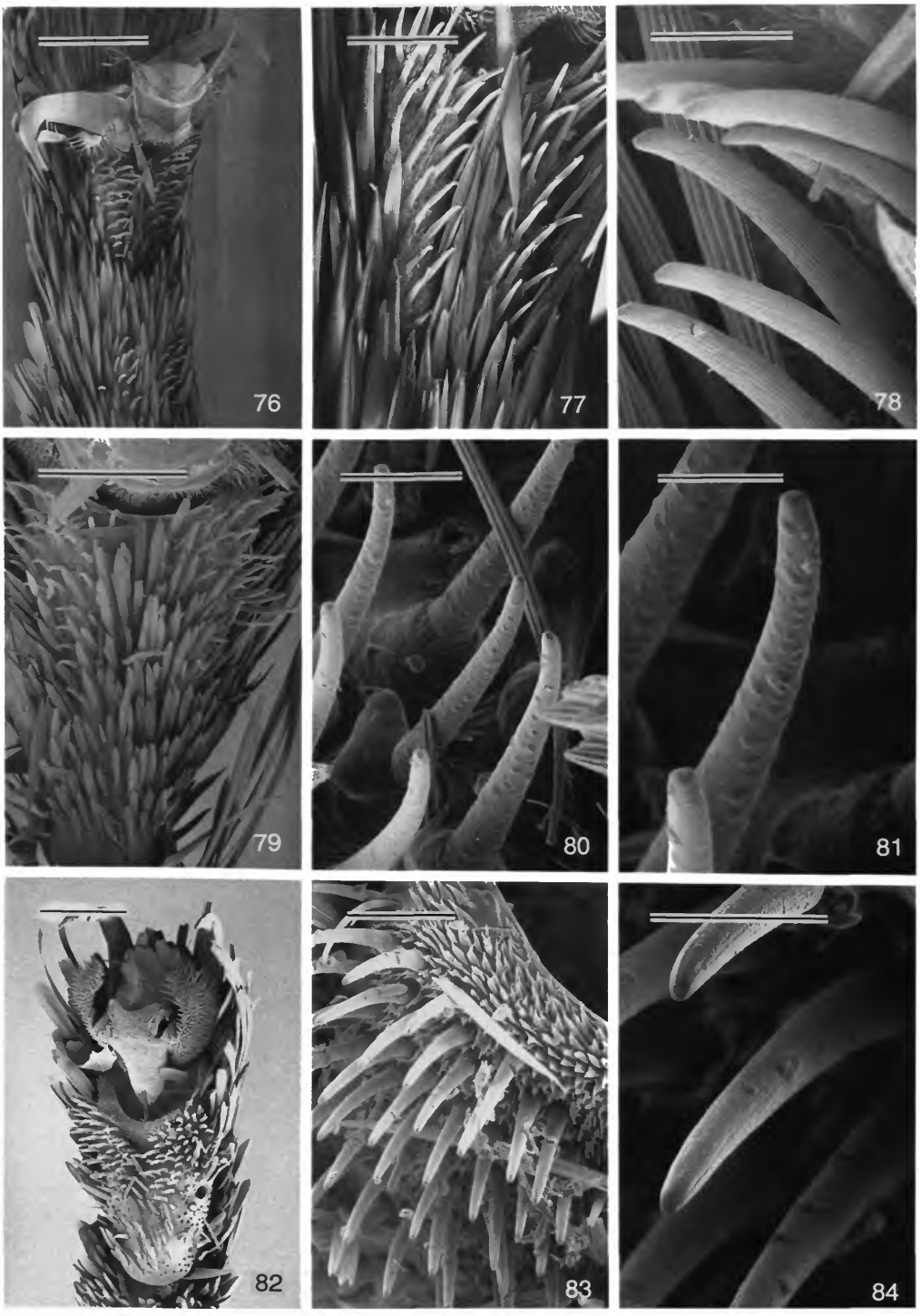
MALE GENITALIA.—The variable nature of the male genitalia throughout the limacodid group makes characters associated with them difficult to describe and homologize. External male genitalia have been described in the Megalopygidae (Eyer, 1924; Hopp, 1927, 1934), Limacodidae (Janse, 1964; Holloway 1986, 1987), Dalceridae (Eyer, 1924; Miller, 1994), Epipyropidae (Jordan, 1928; Heinrich, 1931; Common, 1990), and Cyclotornidae (Common, 1990). The muscles of the male genitalia in the Limacodidae and Zygaenidae were discussed by Kuznetsov and Stekol'nikov (1981), and those in *Podalia albescens* Schaus (Megalopygidae) by Oiticica Filho (1946).

The uncus in the Megalopygidae is narrow and hooked (Figure 351), as in the Zygaenidae (Alberti, 1954). In the Aididae and Limacodidae, the uncus is larger and broader at its base where it connects to the tegumen (Figures 352, 356, 357), as it is in *Somabrachys* (Somabrachyidae) (Jordan, 1916). In the Dalceridae the uncus is highly reduced and has socii (Figures 354, 355); its function is perhaps replaced by the gnathos (Miller, 1994). The vinculum is much wider in the Megalopygidae and Aididae (Figures 351, 352) than it is in the Dalceridae and Limacodidae (Figures 354, 356). The saccus is well developed in the Dalceridae (Figures 354, 355) and Limacodidae (Figure 356), in dalcerids frequently being one-fourth or more the length of the genitalia (Miller, 1994).

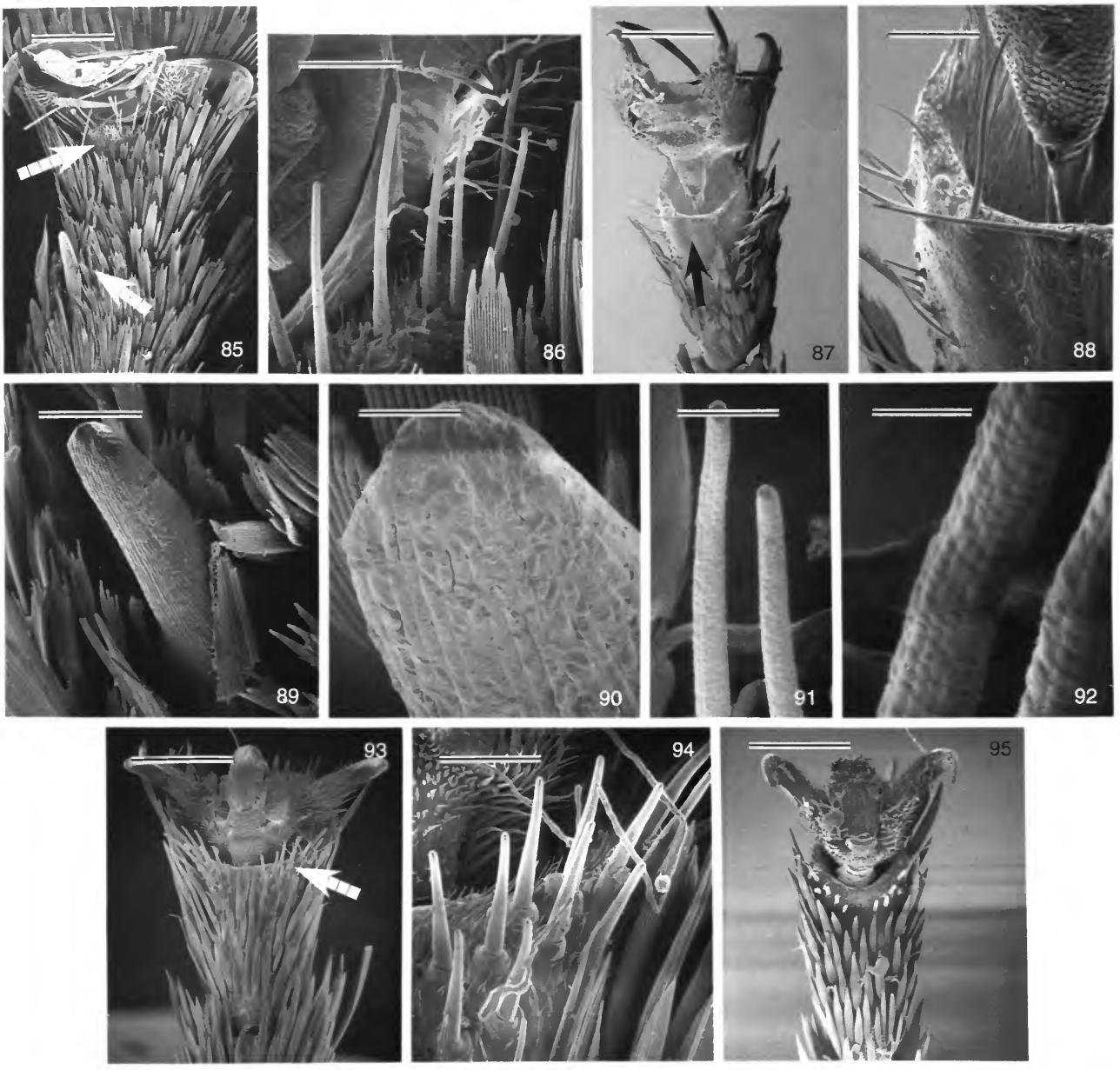
The gnathos was considered by Common (1975) to be independently derived in different groups of Lepidoptera, even within superfamilies. It is simple and lance-shaped in most of the Limacodidae (Figures 356, 357) (Janse, 1964; Holloway, 1986), whereas in the Dalceridae it is sometimes more divided and elaborate (Miller, 1994). Other Zygaenoidea purportedly with a gnathos include the Epipyropidae (Heinrich, 1931) and Cyclotornidae (Common, 1990). The gnathos is absent in the Aididae, Somabrachyidae (Jordan, 1916; Geertsema, pers. comm.), and most of the Megalopygidae; Hopp (1927, fig. 12) reports a gnathos in the Trosiinae (e.g., *Microcladia pygmaea*). Species of Chrysopolominae (sensu nova) have paired transtillar lobes located in a position similar to that of the gnathos (Hering, 1937).

The paired valvae are symmetrical, wide at the base, and entire in the Aididae (Figure 352), Somabrachyidae (Jordan, 1916; Geertsema, pers. comm.), and most Limacodidae (Figures 356, 357), similar to those of Procridinae (Zygaenidae) (Tarmann, 1984). In some limacodids, the valvae are apically emarginate or are deeply split (e.g., *Heuretes,* see Epstein and Miller, 1990, figs. 6, 8). The valvae are extremely reduced in dalcerids (Figures 354, 355) (Miller, 1994). Eyer (1924) and Hopp (1927, 1930) considered the valva in megalopygids to be divided into a dorsal harpe (= cucullus of Eyer) and a ventral sacculus. I treat the dorsal lobe as homologous to the valva, and the ventral lobe as homologous to the medial juxtal lobes found in the Aididae (compare Figures 351 and 352; see "Megalopygidae" for a discussion of the homology of these lobes). Processes on the valva are rare, but they do occur in the Limacodidae, sometimes in conjunction with what may be androconial pouches (e.g., New World *Natada*).

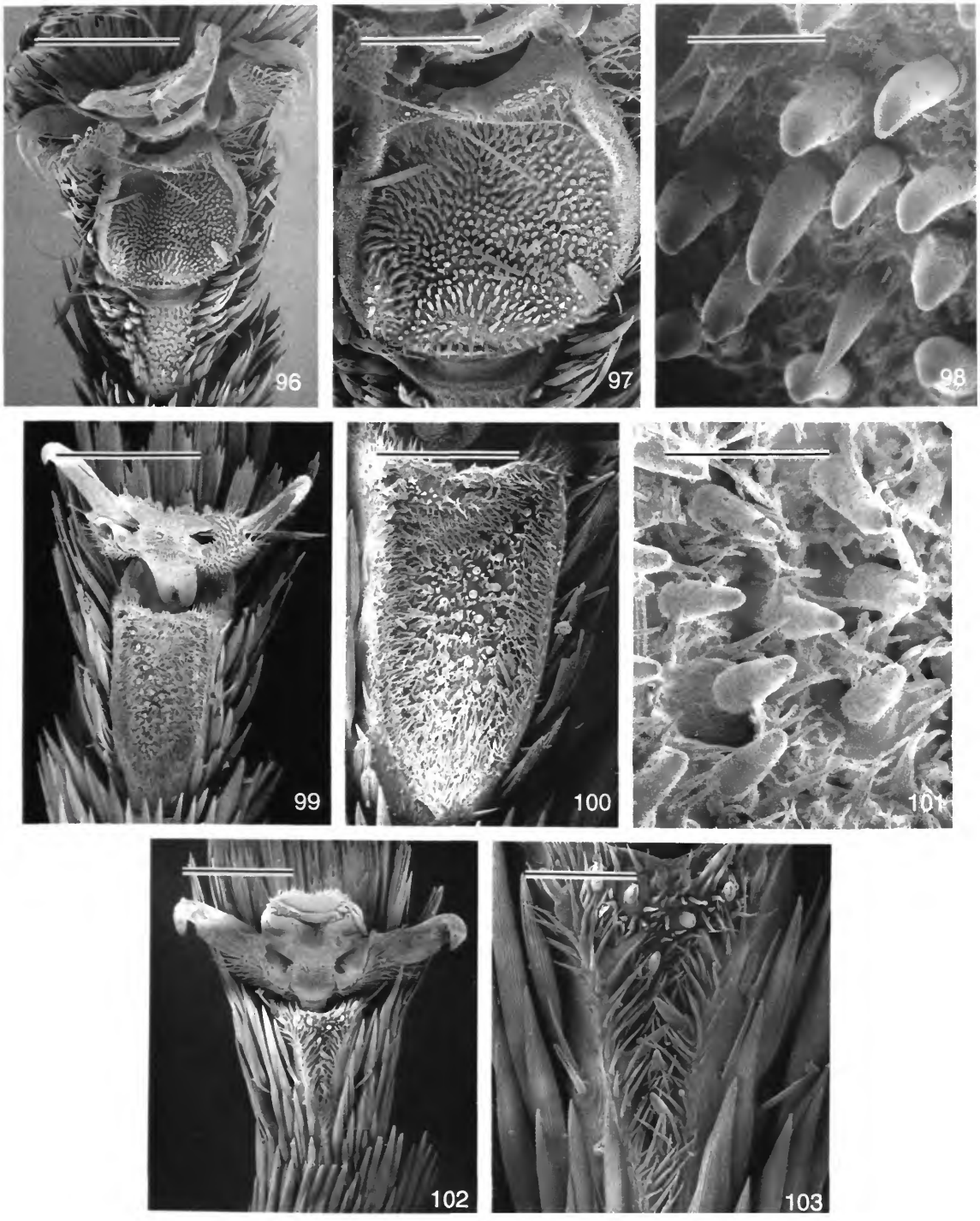
The region between the valva and the aedeagus presents a number of homology problems (Miller, 1994). Various lobes and processes can occur either dorsal or ventral to the aedeagus



FIGURES 76–84.—Female 5th tarsomere and pretarsus of Megalopygidae and Aididae (scale length in parentheses). 76–78, *Norape* sp. (Trosiinae): 76, ventral view of 4th and 5th tarsomere (200 µm); 77, 5th tarsomere (100 µm); 78, sensilla trichodea (20 µm). 79–81, *Megalopyge crispata* (Megalopyginae): 79, 5th tarsomere (200 µm); 80, sensilla trichodea (20 µm); 81, sensilla trichodea (10 µm). 82–84, *Aidos amanda* (Aididae): 82, 5th tarsomere and pretarsus (200 µm); 83, sensilla trichodea (50 µm); 84, sensilla trichodea (20 µm).



FIGURES 85–95.—Fifth tarsomere and pretarsus of Dalceridae and primitive Limacodidae (scale length in parentheses). 85–92, *Dalcera abrasa* (Dalceridae): 85, female pretarsus and 5th tarsomere (upper arrow points to location of sensilla trichodea; lower arrow points to tarsal spur) (200 μm); 86, sensilla trichodea on distal portion of 5th tarsomere in 85 (see upper arrow) (38 μm); 87, male pretarsus and 5th tarsomere (arrow points to distal portion of 5th tarsomere) (200 μm); 88, detail of male pretarsus and distal portion of 5th tarsomere in 87 (see arrow; note absence of sensilla trichodea) (50 μm); 89, tarsal spur on female 5th tarsomere in 85 (see lower arrow) (43 μm); 90, detail of female tarsal spur (10 μm); 91, female sensilla trichodea (10 μm); 92, detail of female sensilla trichodea (4 μm). 93, 94, female *Pantoctaenia prasina* (Limacodidae): 93, pretarsus and 5th tarsomere (arrow points to location of sensilla trichodea) (176 μm); 94, detail of sensilla trichodea in 93 (see arrow) (38 μm). 95, pretarsus and 5th tarsomere of female *Crothaema* sp. (Limacodidae) (150 μm).



FIGURES 96–103.—Female 5th tarsomere and pretarsus of Chrysopolominae and Limacodidae (scale length in parentheses). 96–98, *Strigivenifera venata:* 96, pretarsus and 4th and 5th tarsomeres (500 µm); 97, 5th tarsomere (200 µm); 98, detail of sensilla trichodea (20 µm). 99–101, *Semyra coarctata* complex (Limacodidae): 99, pretarsus and 5th tarsomere (200 µm); 100, 5th tarsomere (100 µm); 101, sensilla trichodea (note spinules) (20 µm). 102, 103, *Apoda biguttata* (Limacodidae): 102, pretarsus and 5th tarsomere (150 µm); 103, 5th tarsomere (note long spinules) (50 µm).

and the anellus surrounding it. Dorsal in the Limacodidae (+ Chrysopolomidae), the transtilla can be simple, a membranous hood, or setose processes (Figure 356), and it is sometimes broadly connected to the anellus. Ventral to the aedeagus, the juxta can be composed of a simple plate, paired processes arising from a plate (Limacodidae; Figure 357), or it can be entirely lobes (Aididae; Figures 352, 353) or processes (Dalceridae; Figures 354, 355).

The aedeagus generally lies parallel to the axis of the abdomen or is only slightly curved; however, in the Limacodidae it is often strongly bent or curved at the base (Holloway, 1986). The Megalopygidae and Zygaenidae (e.g., Procridinae, see Tarmann, 1984) have a broad aedeagus with one or several large nondeciduous cornuti. The Dalceridae (Miller, 1994) and Limacodidae have smaller cornuti in patches or have cornuti absent. In the Limacodidae, the apex of the aedeagus exhibits a wide diversity of shapes and processes.

FEMALE GENITALIA.—Most of the families in the limacodid group have open, disk-shaped papillae anales (ovipositor lobes). In the Limacodidae (+ Chrysopolomidae), the shape of the lateral margins varies from convex (Figure 362) to concave (Figure 363). The Aididae and Dalceridae have the papillae divided equally into dorsal and ventral lobes (Figures 347, 349), although the dorsal lobes are medially fused in aidids.

The ovipositor lobes of megalopygids are medially appressed and laterally flattened (Figures 345, 346) (Holloway, 1986). This is perhaps due to the presence of a dense clump of deciduous piliform scales near the end of the abdomen. Used to cover oviposited eggs, the scales are attached to a membranous A7, which is positioned posteriorly and extends to the middle of A8 (Figure 346).

Other external lobes may be located anteriorly on A8 near the papillae anales, either dorsally or ventrally. These may be sclerotized with intersegmental pouches or may be membranous. Small membranous digitate or pedunculate lateral lobes are present on the eighth segment in many limacodids (Figure 362) (Holloway, 1986; Epstein, 1988) and in chrysopolomines (Figures 363, 364).

Both anterior and posterior apophyses are present in the Megalopygidae (Figure 346), Aididae (Figure 348), and Limacodidae (+ Chrysopolomidae) (Figures 362–364). Anterior apophyses are absent in the Dalceridae (Figure 350) (Miller, 1994).

The bursa copulatrix and its components are quite variable within the limacodid group. This variability includes the length and shape of the corpus and ductus bursae relative to each other and to the spermatheca. In megalopygids the bursa copulatrix may be shorter than segment A8 (Figure 346), whereas a coiled ductus bursae may be either present or absent in limacodids (Holloway, 1986). In the limacodid group, signa have been reported or observed only in Limacodidae thus far.

In addition to sebaceous glands, large "secondary accessory glands" (Petersen, 1900) occur in the Zygaenoidea (Miller, 1993). The term "Petersen's glands" has been applied to these glands in *Zygaena* and in other zygaenine genera (Bode and Naumann, 1988; Naumann, 1988). Naumann (1988) pointed out structural and histological differences between the glands of the Zygaeninae and the Procridinae, although he acknowledged possible homology.

Secondary accessory glands occur in other zygaenoid groups including the Dalceridae (Figure 350) (Miller, 1993), Aididae (Figure 348) (Epstein, 1988), Epipyropidae, and Cyclotornidae (Common, 1990) (see further discussion under each family, below). The glands in dalcerids consist of two independent, pitted, sclerotized, and convoluted lobes. Occupying much of the internal space of A8, each lobe has an external duct leading to the cleft between the upper and lower portions of the papillae anales (Miller, 1993). The glands in aidids differ by being less sclerotized, being broadly connected at the median, and in not having external ducts. Examination of the Limacodidae (Figures 362–364) (see also Naumann, 1988) and Megalopygidae (Figure 346) has not revealed secondary accessory glands in either family.

LARVAE

At rest or in motion, larvae of the limacodid group are characterized by having a greater proportion of their ventral surface area in contact with the substrate than zygaenid larvae do. Reasons for this include (1) the presence of prolegs on segments A2–A7; (2) prolegs that are short relative to the remainder of the ventral surface; (3) the narrowness of the ventral portions of nonproleg segments A8 and A9 (described for megalopygids by Stehr, 1987a); (4) a reduction in the size of the thoracic legs; and (5) the absence of numerous long secondary setae over the lateral and ventral surfaces (excluding megalopygids and somabrachyids).

The larval dorsum exhibits a diversity of conditions in the limacodid group (Figures 1–6). Many species have rows of verrucae, tubercles (scoli), or warts, although these characters are not always homologous (discussed under "Homology and Evolution of Larval Body Setae," below) (see definitions of setal derivatives under "Dorsal and Lateral Body Surfaces," below). In megalopygids and aidids, the cuticle on the thorax and abdomen is shagreened or spinulose throughout except for the membranous pads on megalopygid prolegs (see "Ventral Surface of Body," below). The dorsum and ventrum are mostly smooth in dalcerids and in some limacodids (Figure 7), excluding the anal proleg and the region surrounding the abdominal spiracles.

Limacodid larvae have been termed heteromorphic (= having two or more forms) because the first instar usually differs from the remaining instars in types of setae or in degree of spinosity (Common, 1990). This is exemplified by species having late instars that are smooth-backed and nonurticating. These species have first instars with bisetose tubercles or warts that are lost in subsequent instars (e.g., *Semyra coarctata* complex; compare Figure 170 with Figures 7–9) (Dyar, 1899a). I refer to such change in limacodids simply as

"ontogenetic" because it is not accompanied by major shifts in biology, unlike the parasitic zygaenoid families Epipyropidae and Cyclotornidae, which have hetero- or hypomorphic larvae (Davis, 1987; Common, 1990). Other examples of ontogenetic change include the spinneret in the Limacodidae and the appearance of crochets in post-first instar Dalceridae (Stehr and McFarland, 1985) and *Pantoctaenia* (Limacodidae) (described in "Limacodidae," below).

HEAD.—The dorsum of the head is difficult to observe in preserved larvae because the head is often retracted (Figures 104, 106). Thus, it is best described either in newly hatched larvae, which have a fully extended head (Figures 105, 107), or by removing the head of preserved specimens. The frontoclypeus is indistinct and the epicranial notch may be raised, perhaps to keep the head retracted (Figure 105). Spinules at the base of the head may also serve this function (Figures 107, 108).

Long antennae (Figures 111–116) and a tight arrangement of the stemmata in the Zygaenoidea may be related to the retractile head (Stehr, 1987b; Common, 1990); however, there appears to be variation in stemmata arrangement in both the Zygaenidae and the limacodid group. Stemma 5 is far removed from stemma 4 and is proximate to the antenna in the Somabrachyidae (Figure 118), Megalopygidae (Figure 119), and Aididae (Figures 120, 124). The same is true of *Harrisina americana* (Guérin-Méneville) (Zygaenidae: Procridinae) (Stehr, 1987c), but in *Zygaena trifolii* (Zygaenidae: Zygaeninae) stemma 5 is not disjunct (Figure 117). The Aididae have a gap of approximately the width of a stemma between stemmata 1 and 2 (Figures 120, 124). In the Limacodidae (+ Chrysopolomidae) there is a similar-width gap between stemmata 4 and 5 (Figures 125–128), which is somewhat wider in the Dalceridae (Figure 122).

The Zygaenidae, Megalopygidae, Aididae, and *Psycharium* (Somabrachyidae) each have two S setae, S1 and S2, encircled by stemmata (Figures 117–121). One specimen of *Aidos* sp. was found to have only one stemmatal seta pit on the left side (Figure 124), whereas it had two on the right side (Figure 120). The Limacodidae (+ Chrysopolomidae) and Dalceridae have only one S seta, probably S1 because it is close to stemmata 3 and 4 (Figures 122, 123, 125–128) (based on location given by Stehr, 1987b).

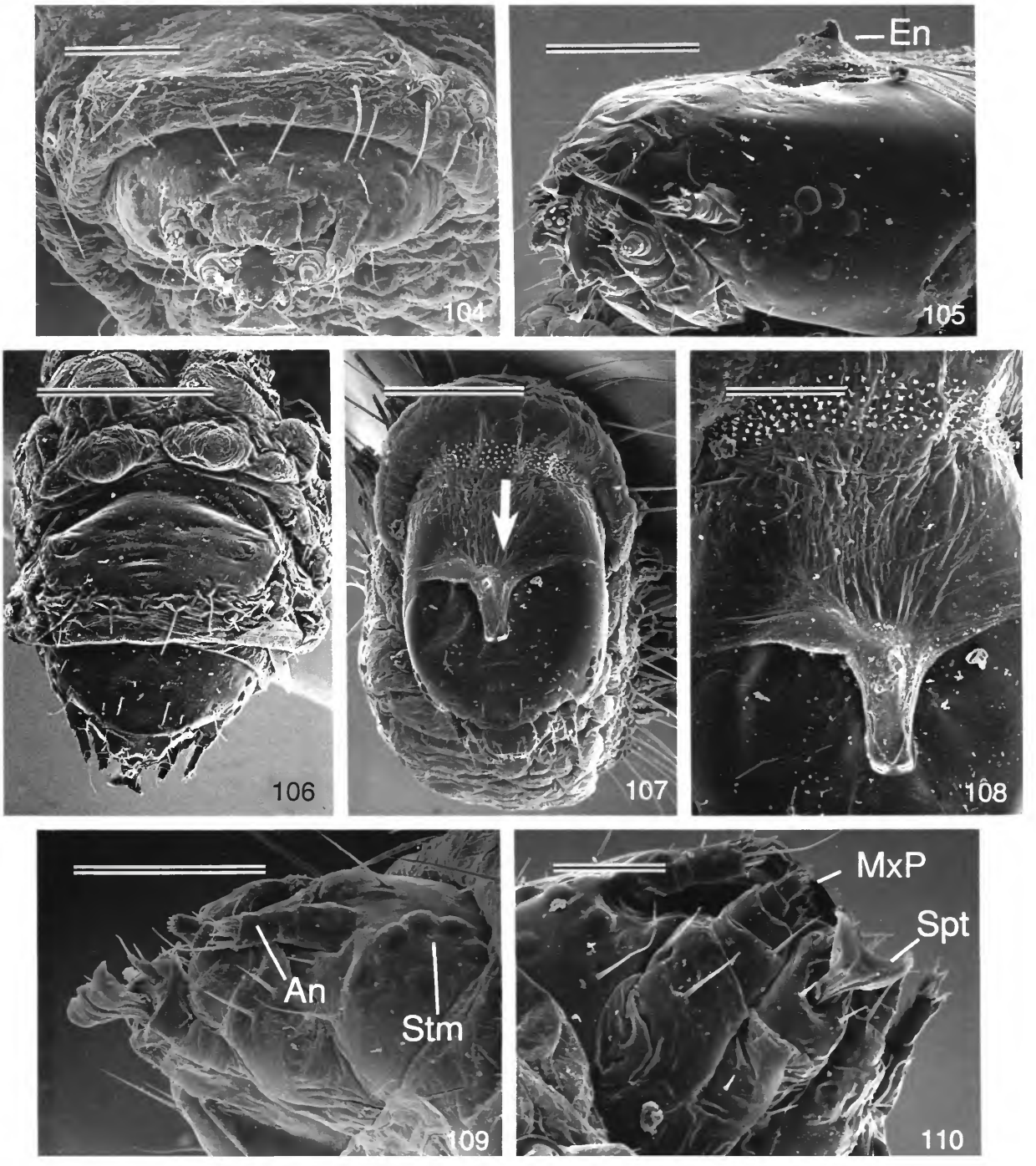
Epipharyngeal spinules in Lepidoptera are usually most abundant beneath the labrum (Figure 130), with few on the margins. This is the case in megalopygids and aidids (Figures 129–133) and in zygaenids. In many limacodids, multiple hair-like spinules occur on the anterior and lateral margins of the labrum as well (Figures 138–141). A similar condition has been reported in gracilleriids, tineids and psychids (Davis et al., 1991), and in phycitine pyralids (Leidy and Neunzig, 1989). The Dalceridae (Figure 134) and *Crothaema* (Limacodidae) have the anterior spinules exclusively on the anteromedial portion of the labrum. Larger and fewer anterior spinules are found in the Aididae (Figure 129) and Megalopygidae (Figure 133). In megalopygids these may be curved under the labrum (Figure 131).

The spinneret in the Zygaenidae, Megalopygidae, and Somabrachyidae is of the tubular type found in most Lepidoptera (Figures 142–147). Aidids have a spinneret with an irregularly shaped tip (Figures 148–151), which may assist in constructing the unusual holes in their cocoons (Figures 15, 17) (Epstein, 1995). Spinnerets in dalcerids (Figures 152–156) and limacodids (Figures 158–162) are usually brush-like, with the apex wider than the base. This general shape was described for *Apoda* (Limacodidae) by Chapman (1894) and Christensen (1950). The dalcerid spinneret shows little ontogenetic change except that in late instars the silk pore, not visible in early instars, appears as a longitudinal slit, and the brush-like anterior margin becomes deeply and evenly cleft (Figure 154) (e.g., *Acraga infusa* complex and *Dalcerina tijucana*). Spinnerets in the Limacodidae, on the other hand, undergo extensive ontogenetic change (see examples and discussion in "Ontogeny and Function of Limacodid Spinnerets").

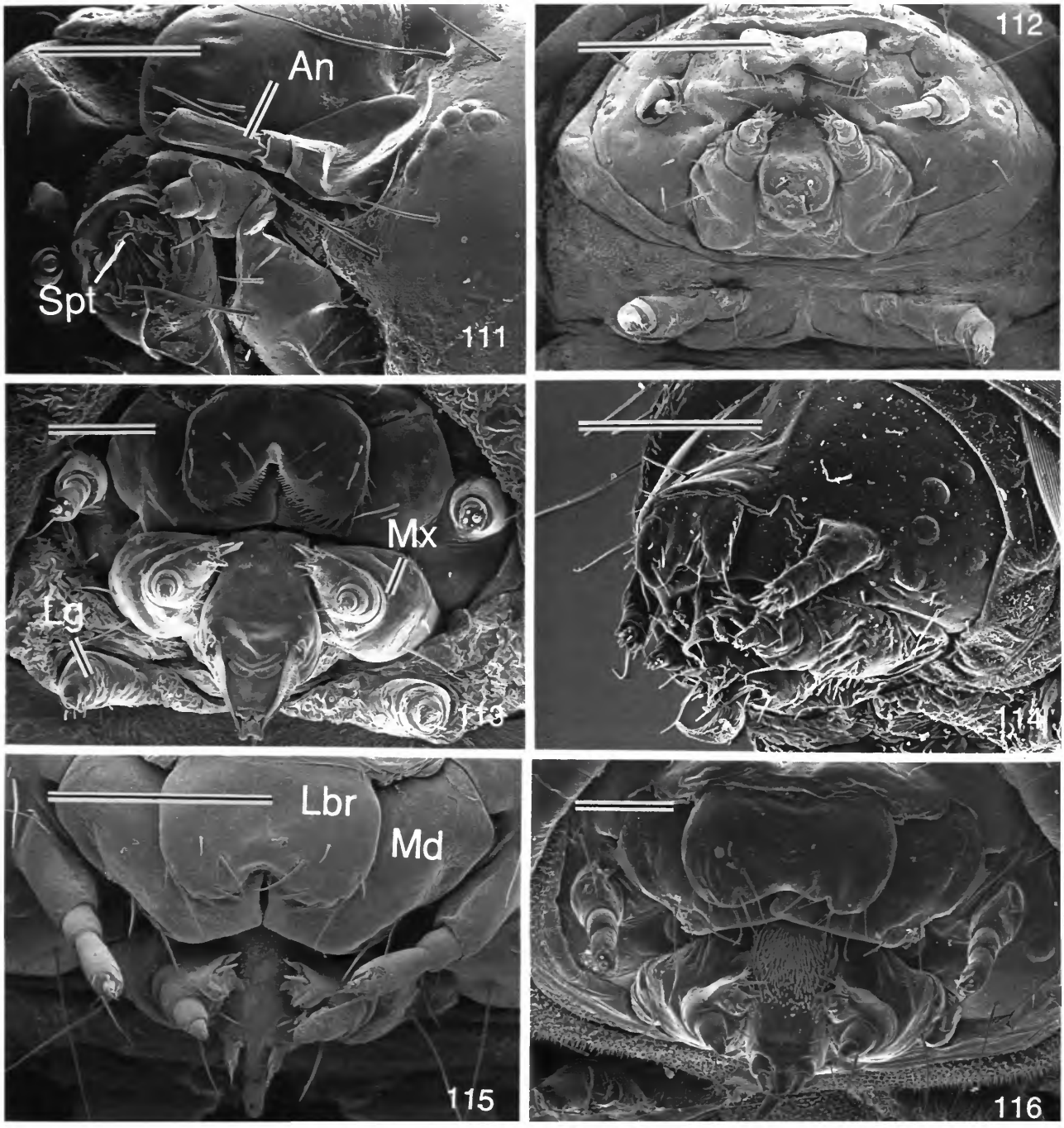
The ventral surface of the spinneret in the limacodid group is divided into three longitudinal bands (Figures 150, 163), with the median part overlying the silk gland channel (the dalcerid silk gland is shown in Figure 157). This occurs whether the spinneret is tubular or brush-like above and also is typical of zygaenids (Figure 143) and most other Lepidoptera (Forbes, 1910).

DORSAL AND LATERAL BODY SURFACES.—Body setae in the limacodid group occur in a wide variety of derivative conditions in addition to the common tactile hair-like condition. These setae may remain unchanged or may undergo changes to derivative forms ontogenetically. Setae are referred to as primary if they appear to correspond to the chaetotaxy found in most Lepidoptera during all instars and are referred to as secondary if they do not (Stehr, 1987b). Examples of setal derivatives herein include tubercles, scoli, verrucae, cuticular warts, and buttons. Tubercles refer to elongate, fleshy (= dilated) setae, often bearing several secondary setae in early instars, and if they persist in late instars they are hairy without urticating setae. Scoli are elongate, fleshy setae that bear urticating setae (= spines). Verrucae are short, wart-like structures that are covered with urticating setae and/or plumose setae. The term tubercle will often be used rather than scolus or verruca when referring to early instars of species with spiny larvae because it cannot be determined whether secondary setae are urticating at this stage. Cuticular warts are naked verrucae or verrucae bearing primary or a few secondary setae. Buttons appear to be tubercles that have undergone reduction. Fungiform setae are tiny dome-shaped setae usually found on the ventral surface but which also occur laterad near spiracles. Gelatinous warts refer to the covering that is secreted by a primary seta rather than to the seta itself.

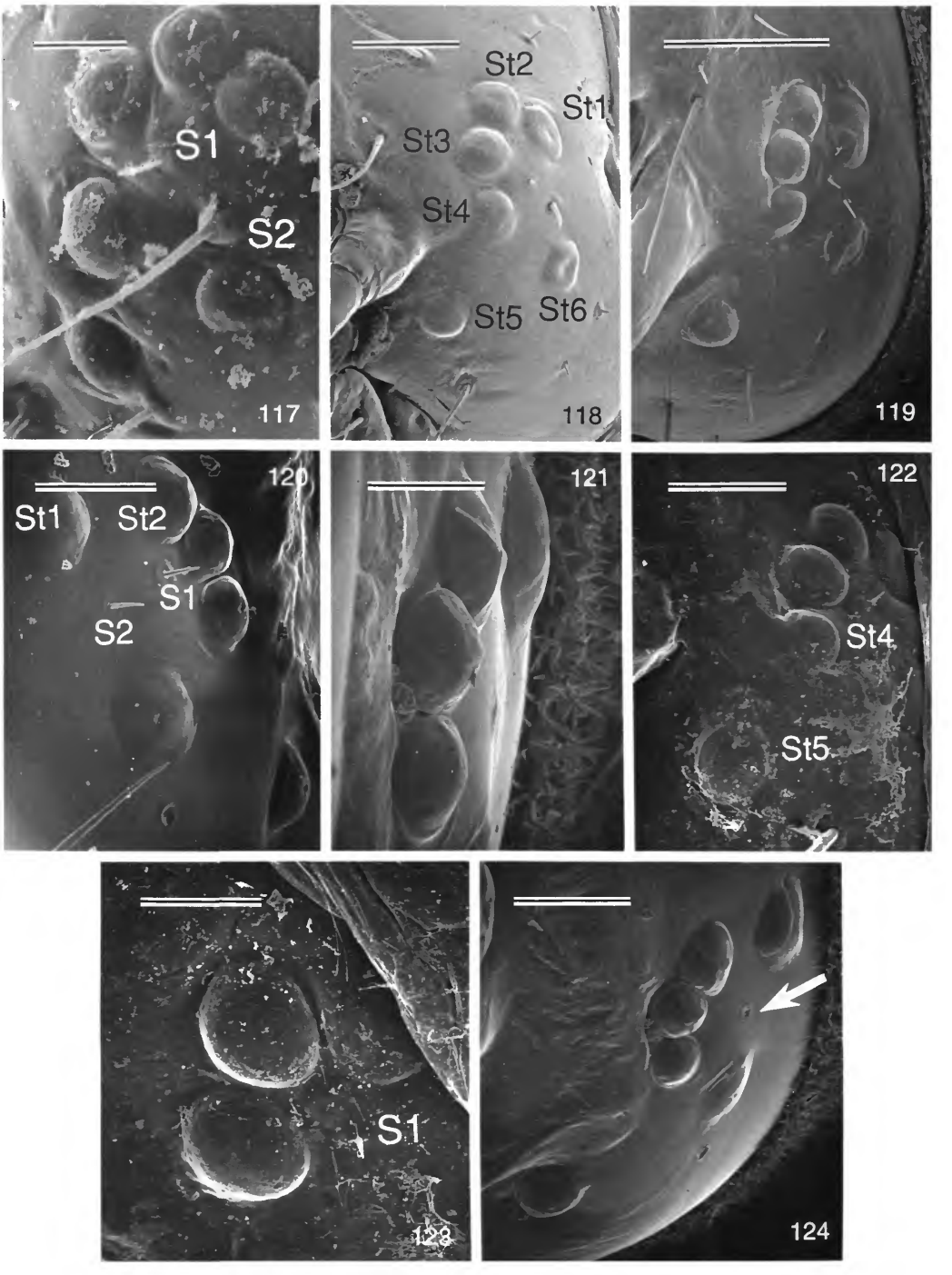
In most limacodid-group families, the prothoracic shield has only primary setae, allowing it to be somewhat retractile into the mesothorax. Megalopygids differ in having a prothoracic shield with verrucae from the first instar onward, making retraction of the prothorax difficult. These verrucae are formed



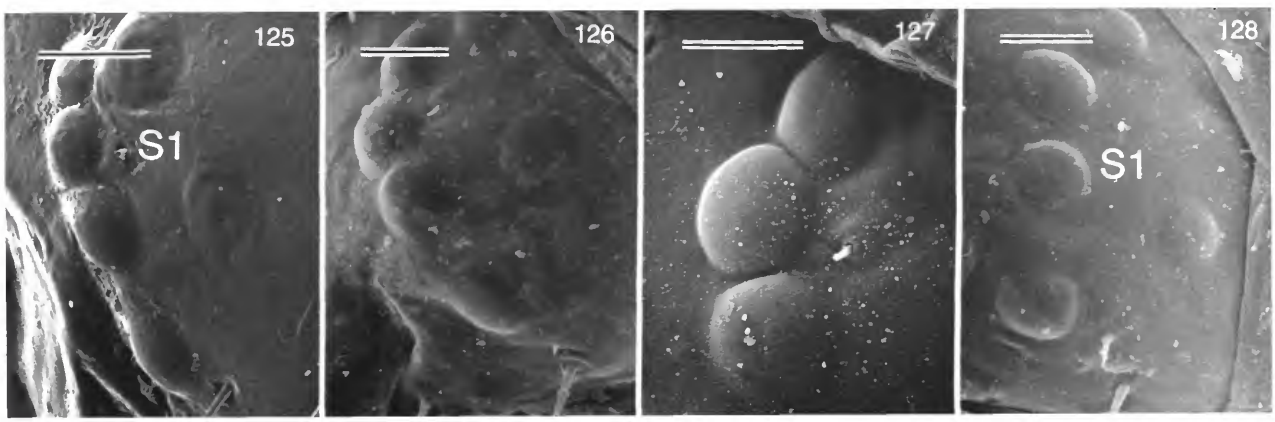
FIGURES 104–110.—Retractile head and prothorax in 1st instar Limacodidae (scale length in parentheses): 104, *Semyra coarctata* complex, frontal view (100 μm); 105, *Phobetron hipparchia*, frontolateral aspect (note epicranial notch above) (100 μm); 106, *Pantoctaenia prasina*, dorsal view of head partially retracted from prothorax (200 μm). 107, 108, *Phobetron hipparchia:* 107, dorsal view of fully retracted head (arrow points to epicranial notch) (200 μm); 108, detail of epicranial notch (note spinules at base of head above) (100 μm). 109, lateroventral view of *Semyra coarctata* complex (100 μm); 110, ventral view of *Pantoctaenia prasina* (50 μm). (An = antenna, En = epicranial notch, MxP = maxillary palpus, Spt = spinneret, Stm = stemmata.)



FIGURES 111–116.—Larval head (scale length in parentheses): 111, *Chrysopoloma similis* (Chrysopolominae), laterofrontal view of ultimate instar exuvia (500 μm); 112, *Acraga infusa* complex (Dalceridae), ~ 4th instar (1 mm); 113, *Semyra coarctata* complex (Limacodidae), 3rd instar (200 μm); 114, *Pantoctaenia prasina* (Limacodidae), 1st instar (100 μm); 115, *Megalopyge crispata* (Megalopyginae), post-third instar (500 μm); 116, *Mesocia pusilla* (Trosiinae), post-first instar (200 μm). (An = antenna, Lbr = labrum, Lg = leg, Md = mandible, Mx = maxilla, Spt = spinneret.)



FIGURES 117–124.—Stemmata (on left side of head unless otherwise indicated) (scale length in parentheses): 117, *Zygaena trifolii* (Zygaenidae) (20 μm); 118, *Psycharium* sp. (Somabrachyidae) (50 μm); 119, *Megalopyge crispata* (Megalopyginae) (200 μm). 120, 121, *Aidos* sp. (Aididae), exuvia from ultimate instar: 120, right side, has S1 and S2 setae (note distance between stemmata 1 and 2) (150 μm); 121, detail of stemmata 1–4 viewed from more frontal perspective (86 μm). 122, 123, *Acraga infusa* complex (Dalceridae): 122, stemma 5 disjunct from stemma 4 (136 μm), 123, detail of stemmata 2, 3 (75 μm). 124, *Aidos* sp. (Aididae), arrow points to only 1 stemmatal seta pit, same individual as in 120 (176 μm). (S1–S2 = stemmatal setae, St1–St6 = stemmata 1–6.)



FIGURES 125–128 (above).—Stemmata of Chrysopolominae and Limacodidae (scale length in parentheses): 125, *Chrysopoloma similis* (100 μm); 126, *Semyra coarctata* complex (20 μm); 127, *Prolimacodes badia*, detail of stemmata 2–4 (15 μm); 128, *Pantoctaenia prasina* (20 μm). (S1 = stemmatal seta.)

from contiguous D and SD rows, whereas L and SV rows are independent (Figure 166). Late instar Zygaenidae and Somabrachyidae frequently have a similar condition, although in several examples, such as *Zygaena trifolii* (Zygaenidae) and *Psycharium* (Somabrachyidae), the first instars have primary setae (Figures 164, 165) that undergo ontogenetic change to form verrucae.

First instar dalcerids and limacodids have T1 spiracles with two closely associated L setae, L1 and L2 (Figures 181–186). Dalcerids sometimes have three L setae in later instars (e.g., *Acraga infusa* complex) (Figures 180, 187). Megalopygids (Stehr, 1987a) and aidids (first instar not observed) have T1 spiracles without proximate, hair-like setae (Figure 338).

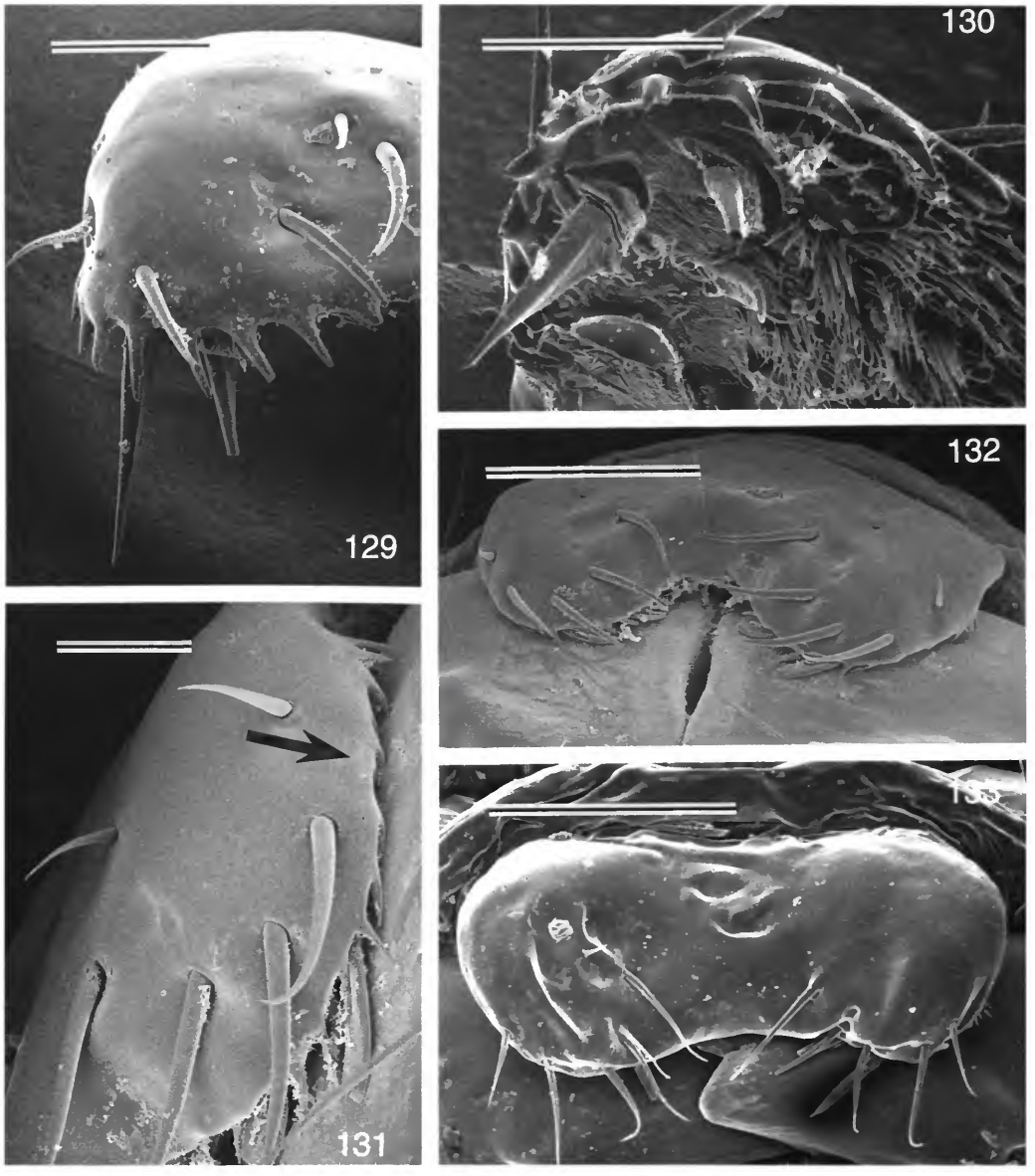
Setae on T2, T3, and the abdomen in the limacodid group occur in a number of different forms. Megalopygids and many zygaenids have D, SD, L, and SV setae as verrucae (Stehr, 1987a, 1987c); however, first instar *Megalopyge* and perhaps all megalopygids differ from first instar *Zygaena trifolii* in the presence of verrucae rather than primary setae. In late instar megalopygids, the D, SD, and L contain both urticating and plumose secondary setae (Figure 169), whereas the SV contains only plumose setae. Late instar *Somabrachys* larvae have urticating and hair-like setae in all positions. Spiny limacodids, dalcerids, and aidids have very different setal modifications or coverings in the D and SD positions compared to the primary tactile setae in the L and, in the first two families, the SV positions.

In dalcerids all D and SD setae on the thoracic and abdominal segments, except T1 and A10, have a translucent, gelatinous covering (Figures 3, 180). On the same segments, limacodid first instars have rows of warts or tubercles (Figures 170–176, 178, 179, 181) in the D and SD positions. These often change form in later instars. For example, species with smooth larvae and simple setae in late instars have first instars with long-branched or unbranched tubercles (Figures 178, 179, 195–203) or warts, with or without setal remnants (Figures 188–192).

Limacodid first instars in spiny species have from three to seven setae per tubercle (Figures 172, 174); these tubercles become either scoli or verrucae in later instars (see more detailed figures below in "Homology and Evolution of Larval Body Setae"). Many species in the *Parasa* complex have deciduous patches of defensive setae located at the bases of D scoli on A8 and A9 (Dyar, 1899a). These are also incorporated into the silk of the cocoon.

Limacodid species of the *Phobetron* complex (Figures 198–203) have tubercles different from species with smooth larvae or species with spiny larvae. First instars have long tubercles similar to those found in smooth larvae (e.g., *Apoda* complex), but the tubercles are retained rather than converted into simple, hair-like setae as in later instars of smooth larvae. In several respects tubercles of late instars in the *Phobetron* complex differ from scoli in spiny larvae. They are covered with branched nonstinging setae, sometimes with urticating setae at the base (e.g., *Heuretes*, Epstein and Miller, 1990). Tubercles of *Phobetron* species are completely detachable in later instars and are incorporated into the cocoon (Dyar, 1896a:184).

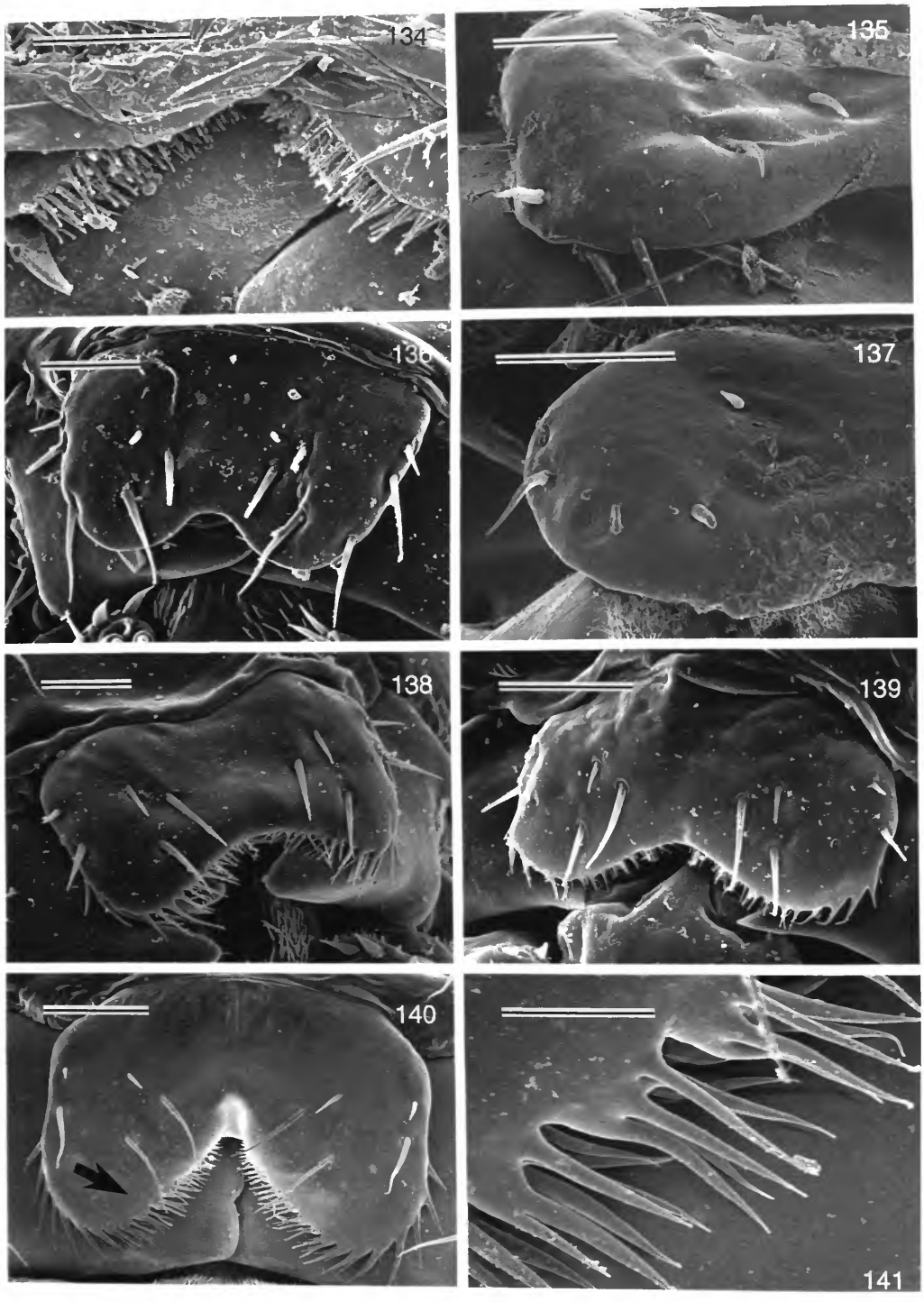
Tubercles of first instar limacodids are everted in the egg and at hatching (Figures 196, 201, 202), telescoping outward soon after (Figures 195, 203). This has been described for *Apoda limacodes* (Hufnagel) (as *Limacodes testudo* (Denis and



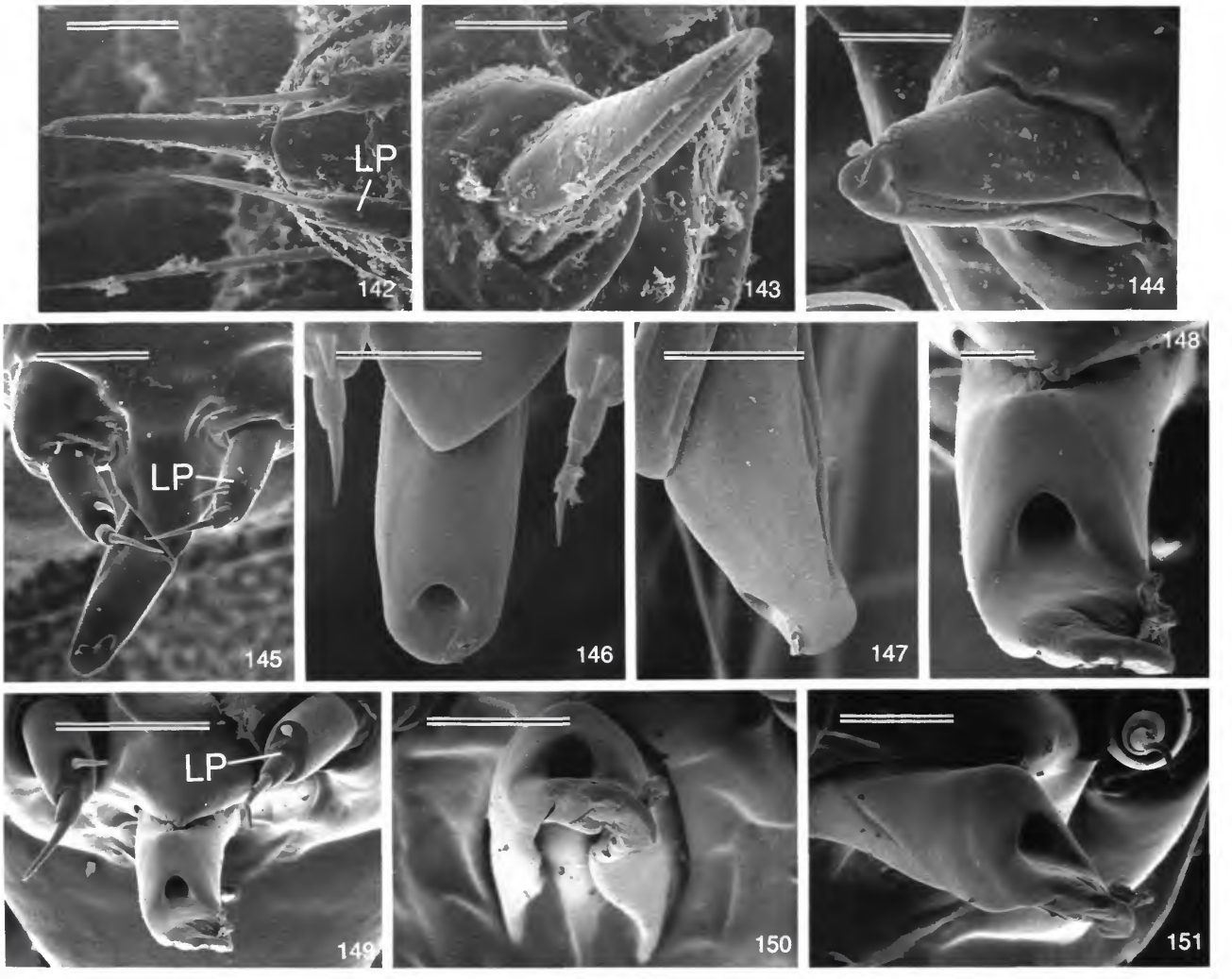
FIGURES 129–133.—Larval labrum of Aididae and Megalopygidae (scale length in parentheses). 129, 130, *Aidos* sp. (Aididae), ultimate instar exuvia: 129, dorsum (100 μm); 130, ventral aspect, showing spinules (100 μm). 131, 132, *Megalopyge crispata* (Megalopyginae): 131, detail of left side, arrow points to spines that are curved under (50 μm); 132, labrum and mandibles (200 μm). 133, *Mesocia pusilla* (Trosiinae) (200 μm).

Schiffermüler) in Chapman, 1894:346; Christensen, 1950), as well as for other species in the *Apoda* and *Phobetron* complexes (Dyar and Morton, 1895:152; Dyar, 1899c:204).

Zygaenids and megalopygids have L and SV verrucae on the abdomen. In post-first instar *Zygaena trifolii*, Tremewan (1985) refers to verrucae on the outer portion of the proleg base as L3, with L1 and L2 below the spiracle in that order. This interpretation differs from Stehr (1987a, 1987c), who defines verrucae on the outer portion of the proleg base in megalopygids and zygaenids as SV setae. I follow Stehr's system



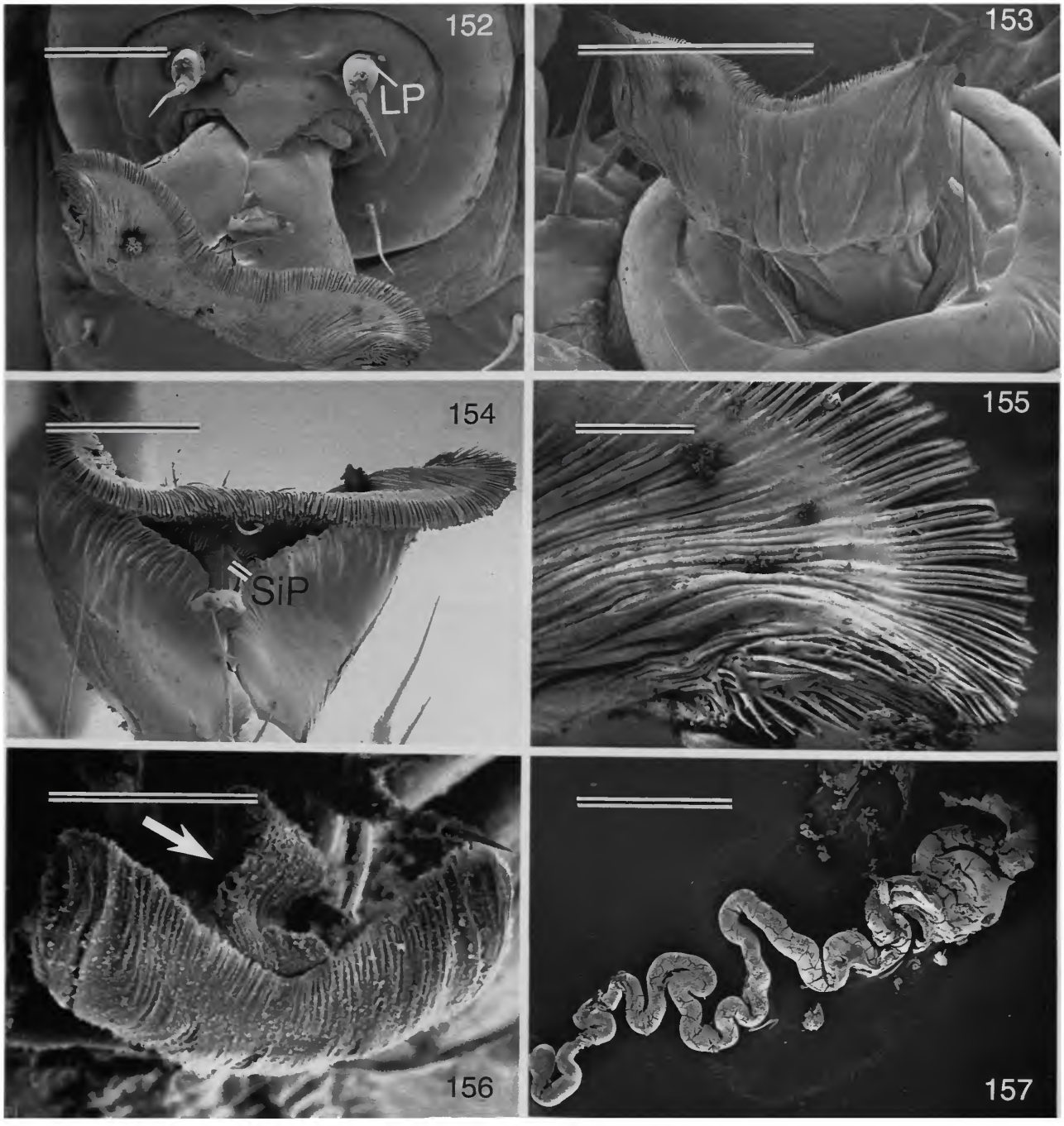
FIGURES 134–141.—Larval labrum of Dalceridae, Chrysopolominae, and Limacodidae (scale length in parentheses): 134, *Dalcerides ingenita* (Dalceridae), post-first instar (20 μm); 135, *Acraga infusa* complex (Dalceridae), late instar (100 μm); 136, *Pantoctaenia prasina* (Limacodidae), 1st instar (20 μm); 137, *Chrysopoloma similis* (Chrysopolominae), prepupal exuvia (200 μm); 138, *Phobetron hipparchia* (Limacodidae), 1st instar (20 μm); 139, *Talima postica* (Limacodidae), 1st instar (20 μm). 140, 141, *Semyra coarctata* complex (Limacodidae): 140, 3rd instar, (100 μm); 141, detail of 140 (see arrrow) (20 μm).



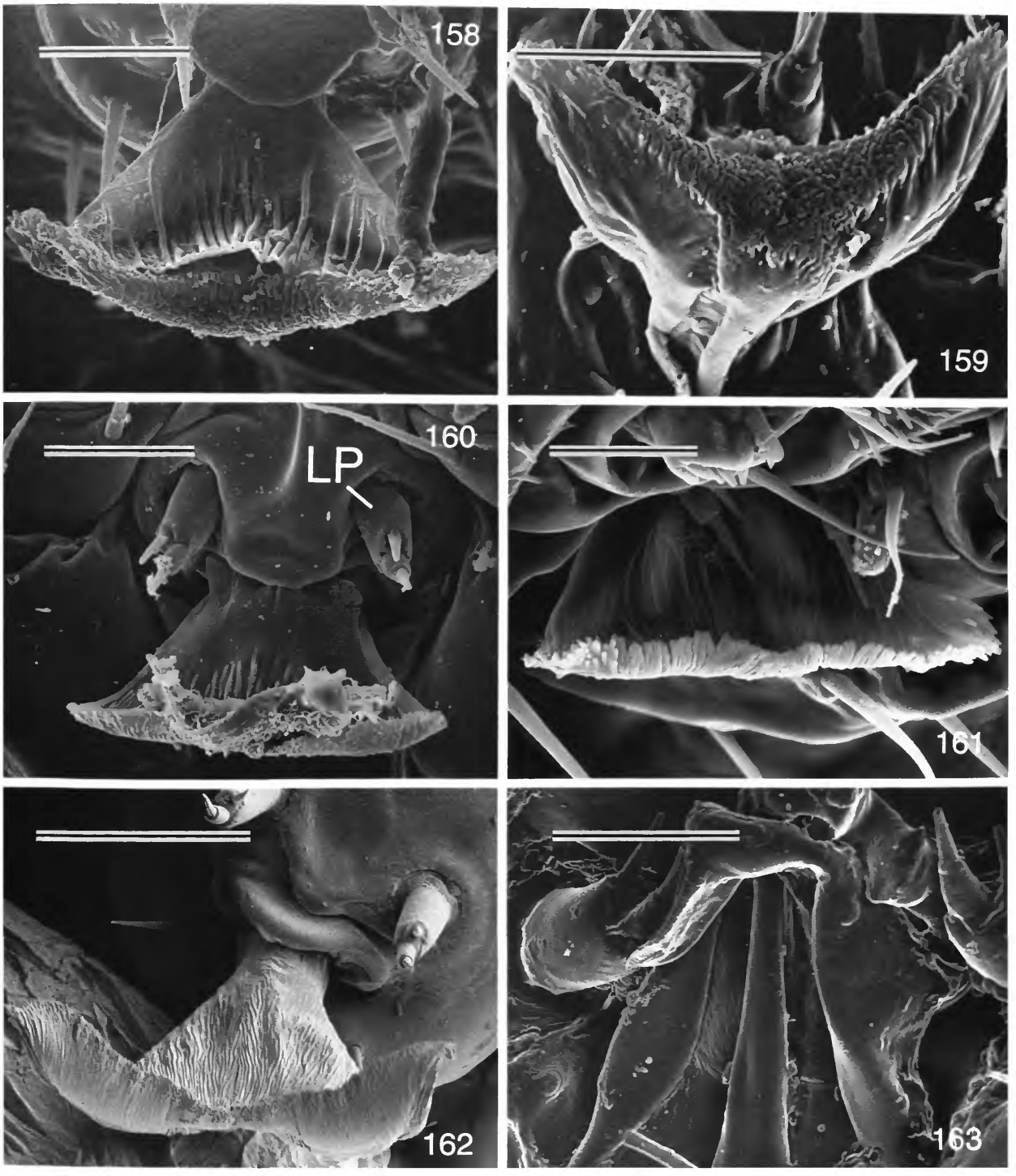
FIGURES 142–151.—Larval spinneret in Zygaenidae, Somabrachyidae, Megalopygidae, and Aididae (scale length in parentheses). 142, 143, *Zygaena trifolii* (Zygaenidae): 142, dorsal view (17.6 μm); 143, lateroventral view (7.5 μm). 144, *Psycharium* sp. (Somabrachyidae), lateroventral view (8.6 μm); 145, *Mesocia pusilla* (Trosiinae), dorsal view (50 μm). 146, 147, *Megalopyge crispata* (Megalopyginae): 146, dorsal view (50 μm); 147, lateral view (50 μm). 148–151, *Aidos* sp. (Aididae), exuvia from ultimate instar: 148, detail of tip and silk pore, dorsal view (20 μm); 149, dorsal view (100 μm); 150, frontoventral view (50 μm); 151, frontolateral view (50 μm). (LP = labial palpus.)

because there appear to be L3 verrucae anterodorsal to the proleg base in the Megalopygidae (e.g., *Megalopyge lanata*, Figure 406). In aidid larvae there is an L3 wart in the same position, with the two L setae proximoventral to the spiracles being L1 and L2 (Figure 407). L3 warts may form part of the flexible ventral surface found in the limacodid + dalcerid clade (see further discussion in "Homology of Suckers," below).

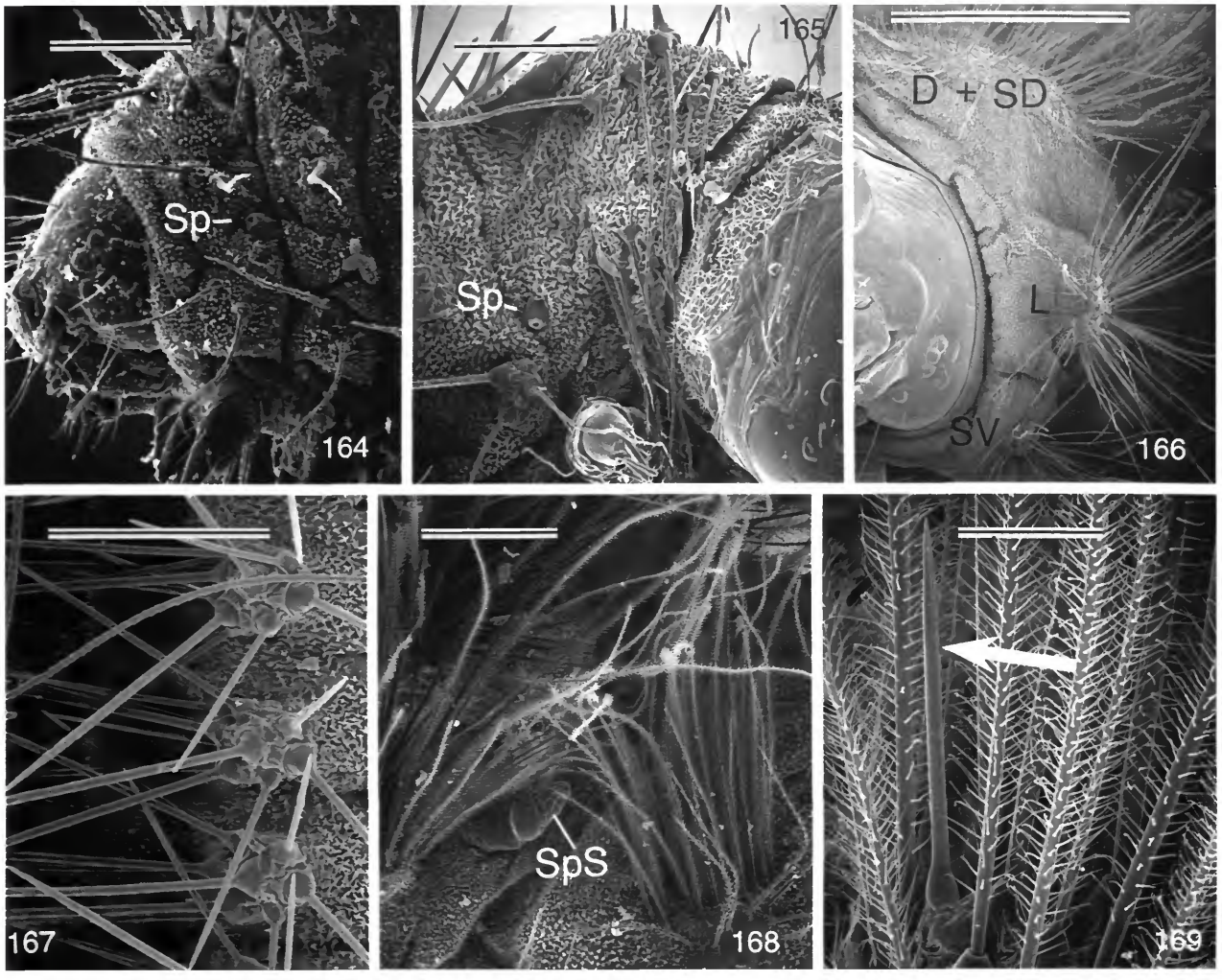
Limacodids and dalcerids (Figures 204–214) and aidids have mostly primary L and SV setae on the abdomen. In *Pantoctaenia* (Limacodidae) and aidids, the abdominal L1 and L2 setae are hair-like and are borne on one (Figure 213) or two warts (Figure 407) proximoventral to the spiracles. In some limacodids, the dorsal abdominal L1 seta is hair-like, whereas the ventral L2 seta is fungiform (Figure 205). Other L setae in limacodids are spatulate (Figure 204), long (Figure 207), or shagreened (Figures 199, 212). In first instar *Crothaema* (Limacodidae), the abdominal L1 setae are similar in appearance to warts in the D and SD rows (Figure 214).



FIGURES 152–157.—Larval spinneret in Dalceridae (scale length in parentheses). 152–155, *Acraga infusa* complex, late instar: 152, frontal view (100 μm); 153, ventral view (200 μm); 154, dorsal view (100 μm); 155, detail of anterior margin (20 μm). 156, dalcerid sp. 1st instar, Ecuador (20 μm) (arrow points to ribbon-like silk); 157, silk gland from *Acraga infusa* complex, late instar (2 mm). (LP = labial palpus, SiP = silk pore.)

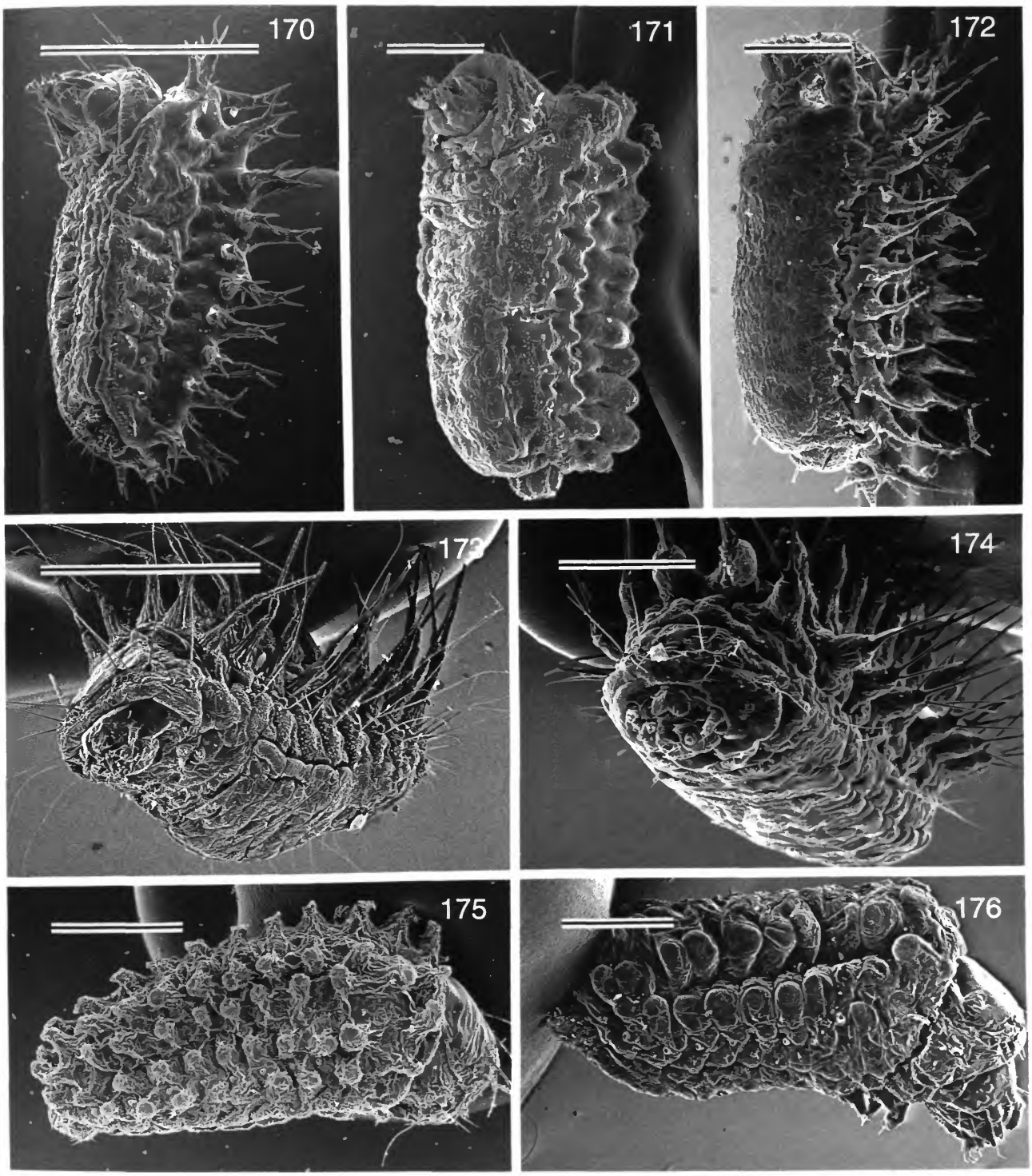


FIGURES 158–163.—Larval spinneret in Limacodidae and Chrysopolominae (1st instar unless otherwise indicated; scale length in parentheses). 158, 159, *Pantoctaenia gemmans:* 158, dorsal view (13.6 μm), 159, ventral view (20 μm). 160, *Prolimacodes badia*, dorsal view (20 μm); 161, *Heuretes* sp., dorsal view (12 μm); 162, *Natada subpectinata*, frontodorsal view, 3rd or 4th instar (50 μm); 163, *Chrysopoloma similis*, ventral view, from exuvia of ultimate instar (100 μm). (LP = labial palpus.)



FIGURES 164–169 (above).—Larval setae and verrucae of Zygaenidae, Megalopygidae, and Somabrachyidae (1st instar unless otherwise indicated; scale length in parentheses). 164–166, prothoracic setae: 164, *Zyagaena trifolii* (136 μm); 165, *Psycharium* sp. (Somabrachyidae) (150 μm); 166, *Mesocia pusilla* (Trosiinae), post-third instar (1 mm). 167, *Psycharium* sp., urticating setae in verrucae, dorsal row (top of photo is anterior) (200 μm). 168, 169, *Mesocia pusilla*, post-third instar, SD verrucae: 168, thorax and abdomen (anterior to left) (231 μm); 169, detail of abdominal verruca (arrow points to urticating seta among plumose setae) (50 μm). (D, L, SD, SV = dorsal-, lateral-, subdorsal-, and subventral-group verrucae, Sp = spiracle, SpS = spiracular sensillum.)

FIGURES 170–176 (opposite page).—Larval habitus of 1st instar Limacodidae (scale length in parentheses): 170, *Semyra coarctata* complex (500 μm); 171, *Belippa horrida* (200 μm); 172, *Euprosterna* sp. (200 μm); 173, *Phobetron hipparchia* (500 μm); 174, *Talima postica* (200 μm); 175, *Crothaema* sp. (200 μm); 176, *Pantoctaenia prasina* (200 μm).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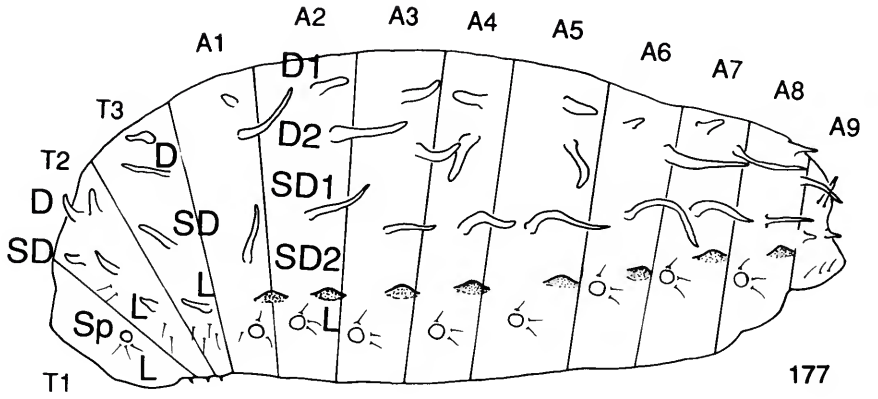
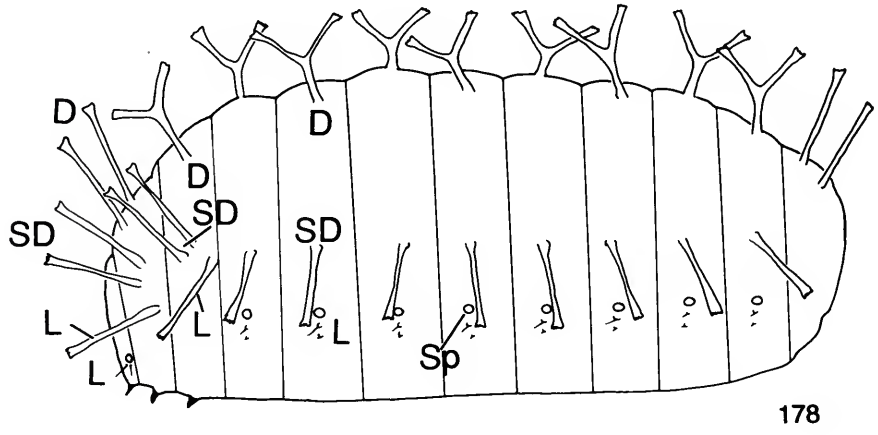
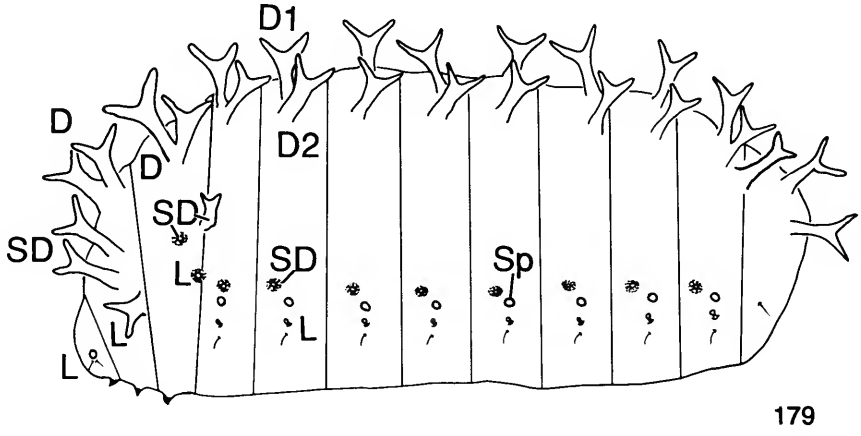
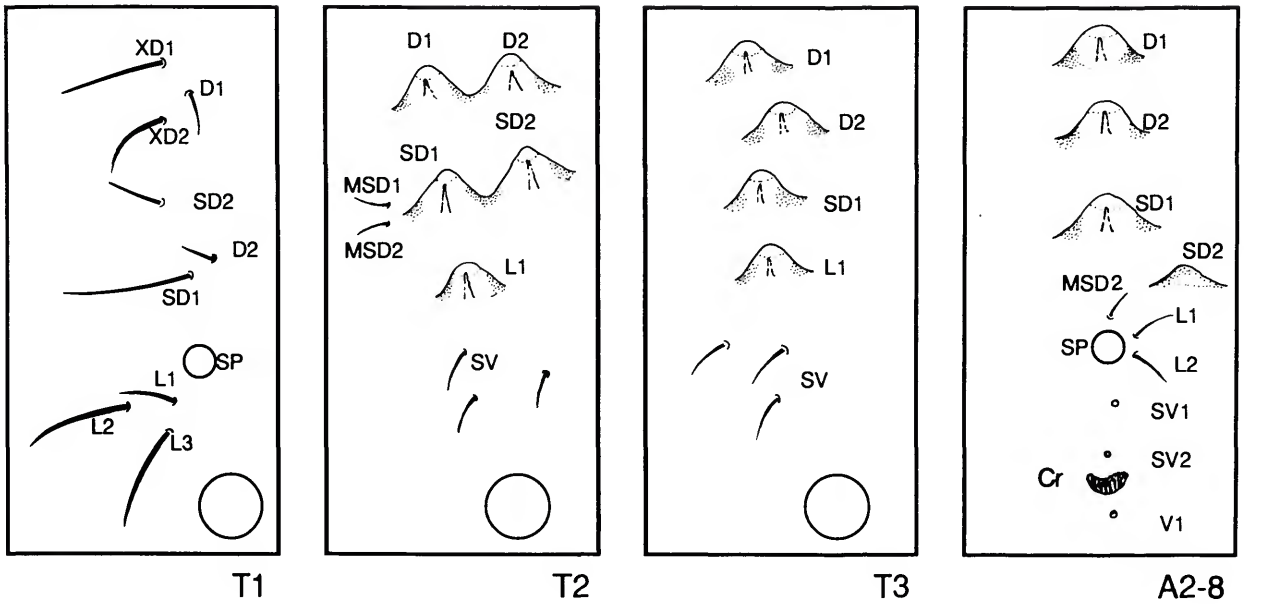
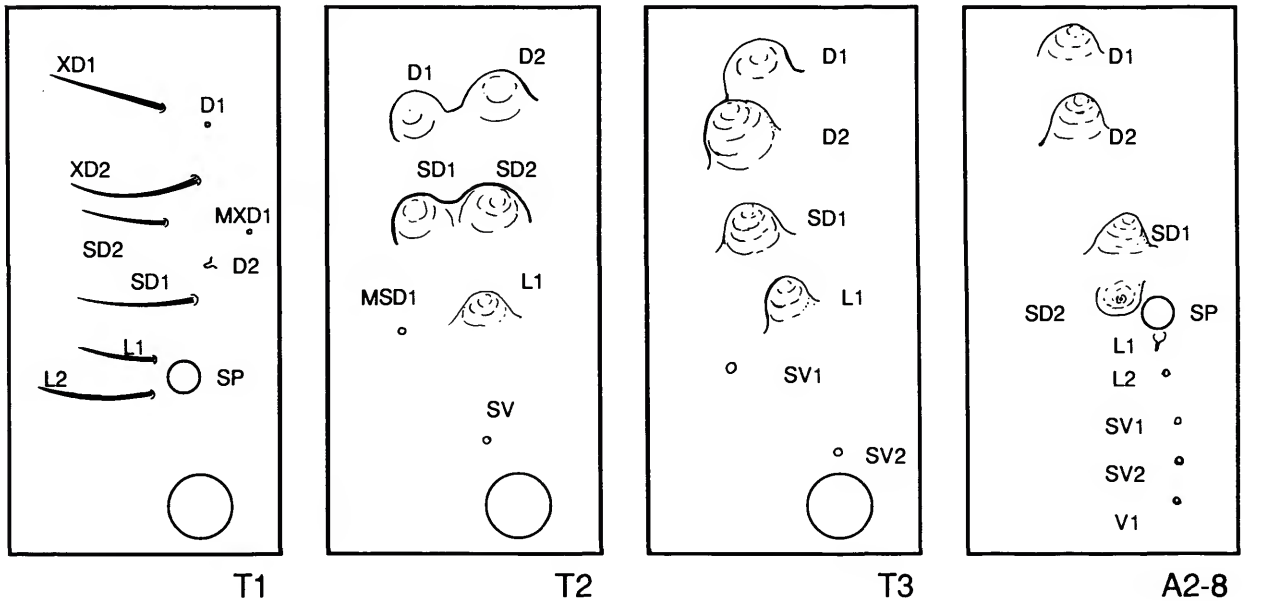




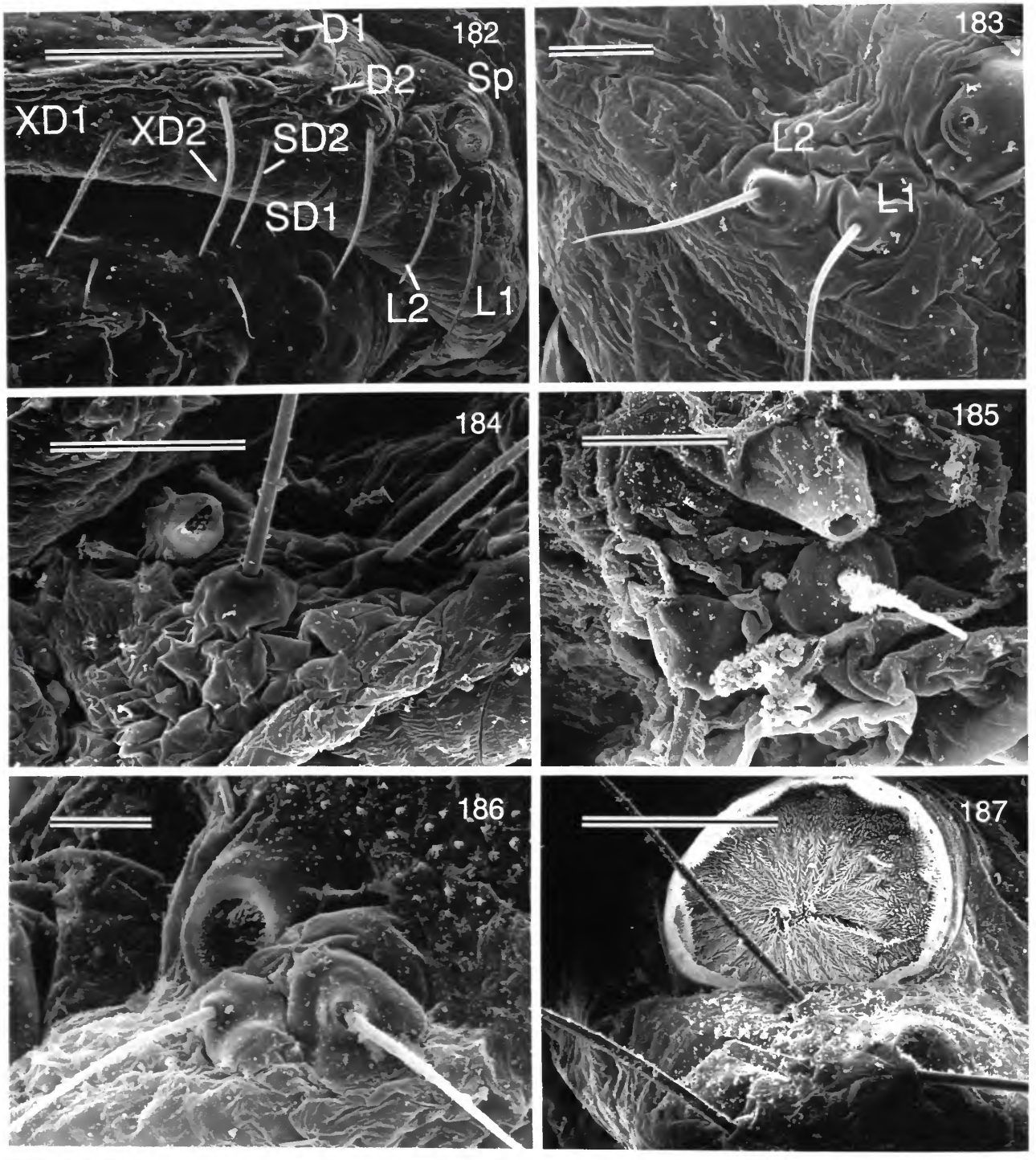


FIGURES 177–179.—Body setae in Dalceridae and 1st instar Limacodidae (semidiagrammatic): 177, *Acraga infusa* complex (Dalceridae), post-third instar (wart-like covering removed); 178, *Tortricidia pallida* Herrich-Schäffer (after Dyar, 1896b; L setae added); 179, *Semyra coarctata* complex. (A1–A9 = abdominal segments 1–9, D, L, SD = dorsal-, lateral-, and subdorsal-group setae, Sp = spiracle, T1, T2, T3 = pro-, meso-, and metathorax.)

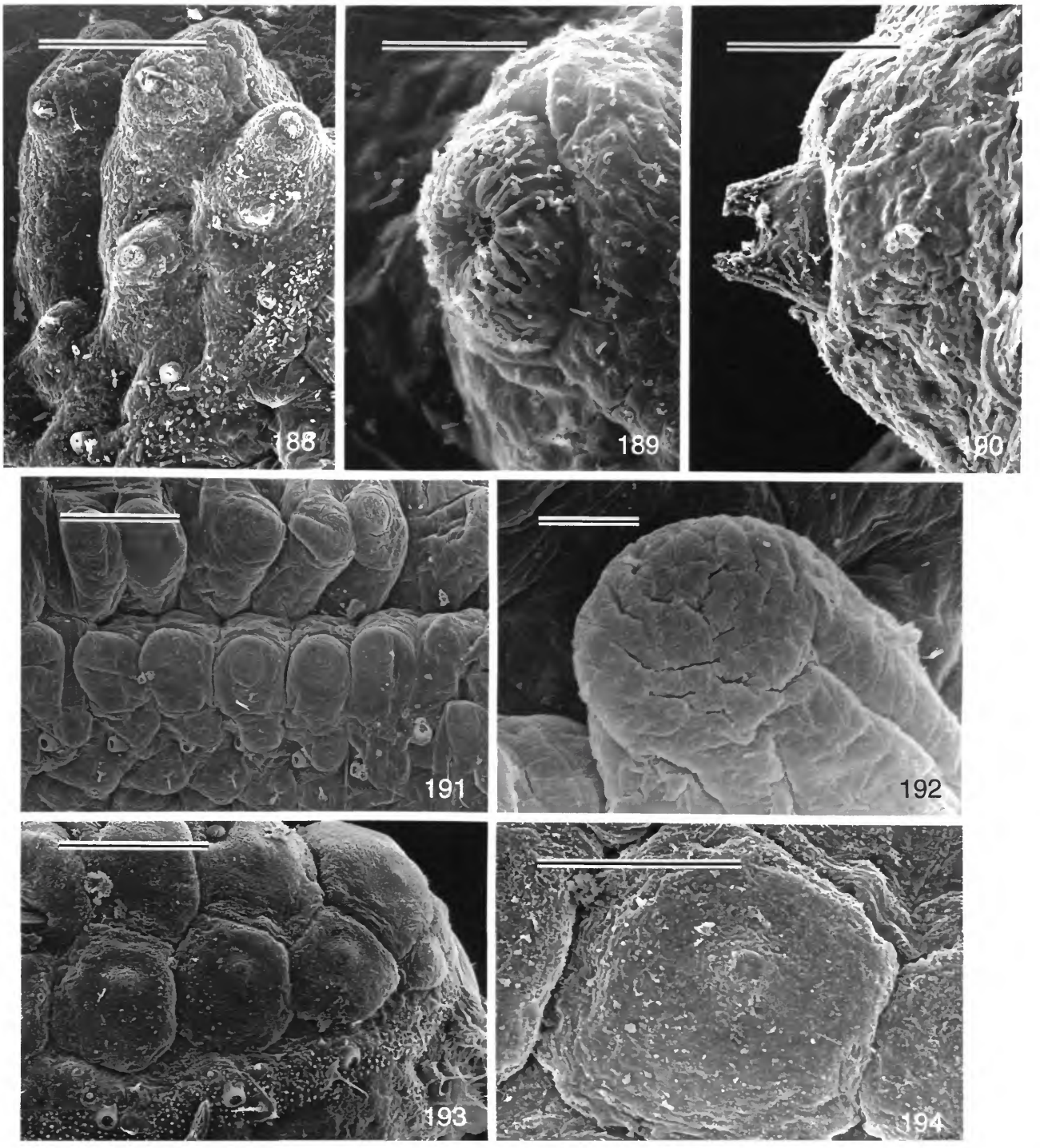




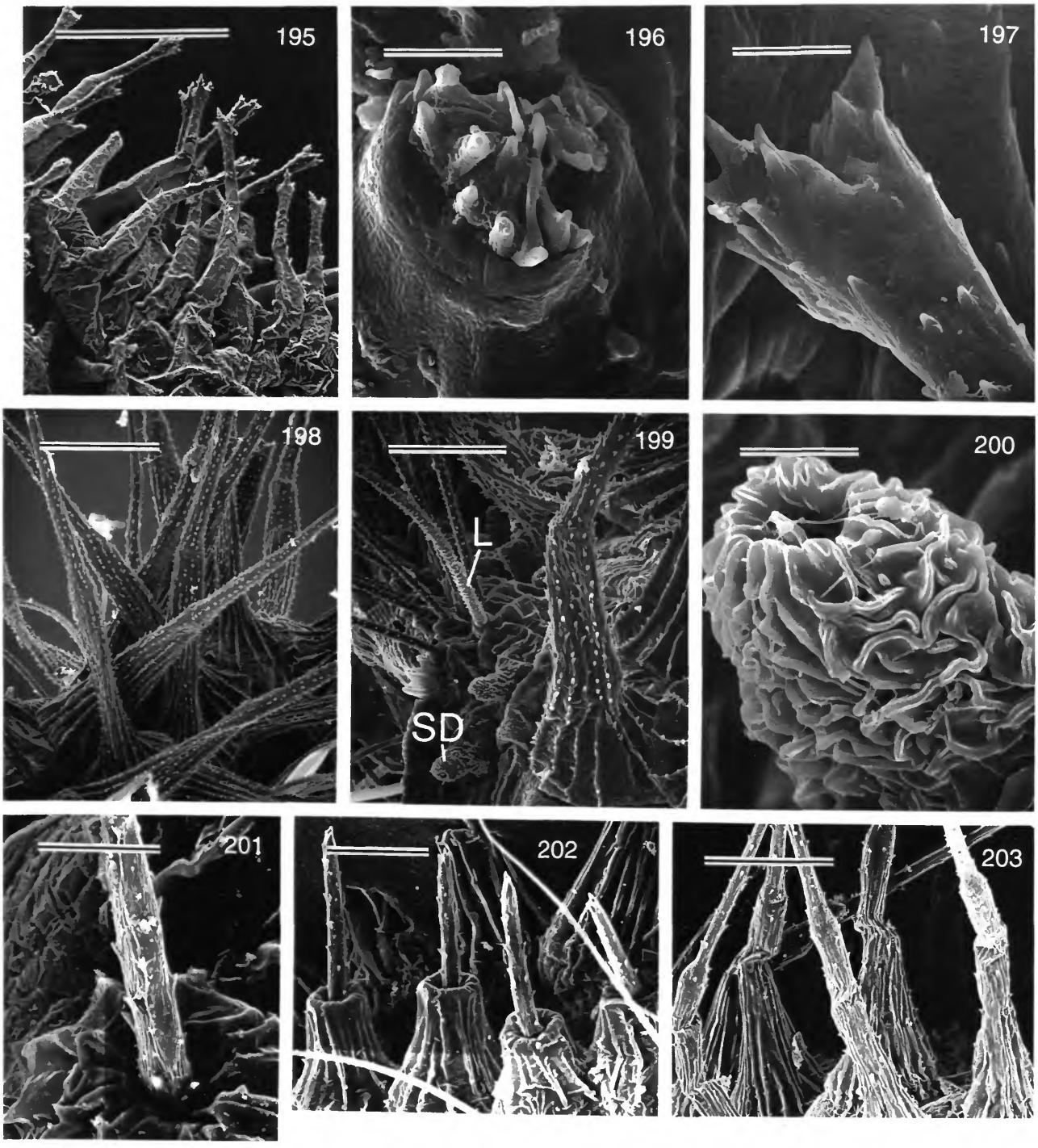
FIGURES 180, 181.—Maps of body setae in late instar Dalceridae and 1st instar Limacodidae: 180, Dalceridae; 181, Limacodidae (T1 = *Semyra coarctata* complex; others = *Pantoctaenia prasina*). (A2–A8 = abdominal segments 2–8, Cr = crochets, D, L, MSD, SD, SV, V, XD = dorsal-, lateral-, subdorsal-proprioceptor-, subdorsal-, subventral-, ventral, and X-dorsal-group setae, MXD = proprioceptor seta, SP = spiracle, T1, T2, T3 = pro-, meso- and metathorax.)



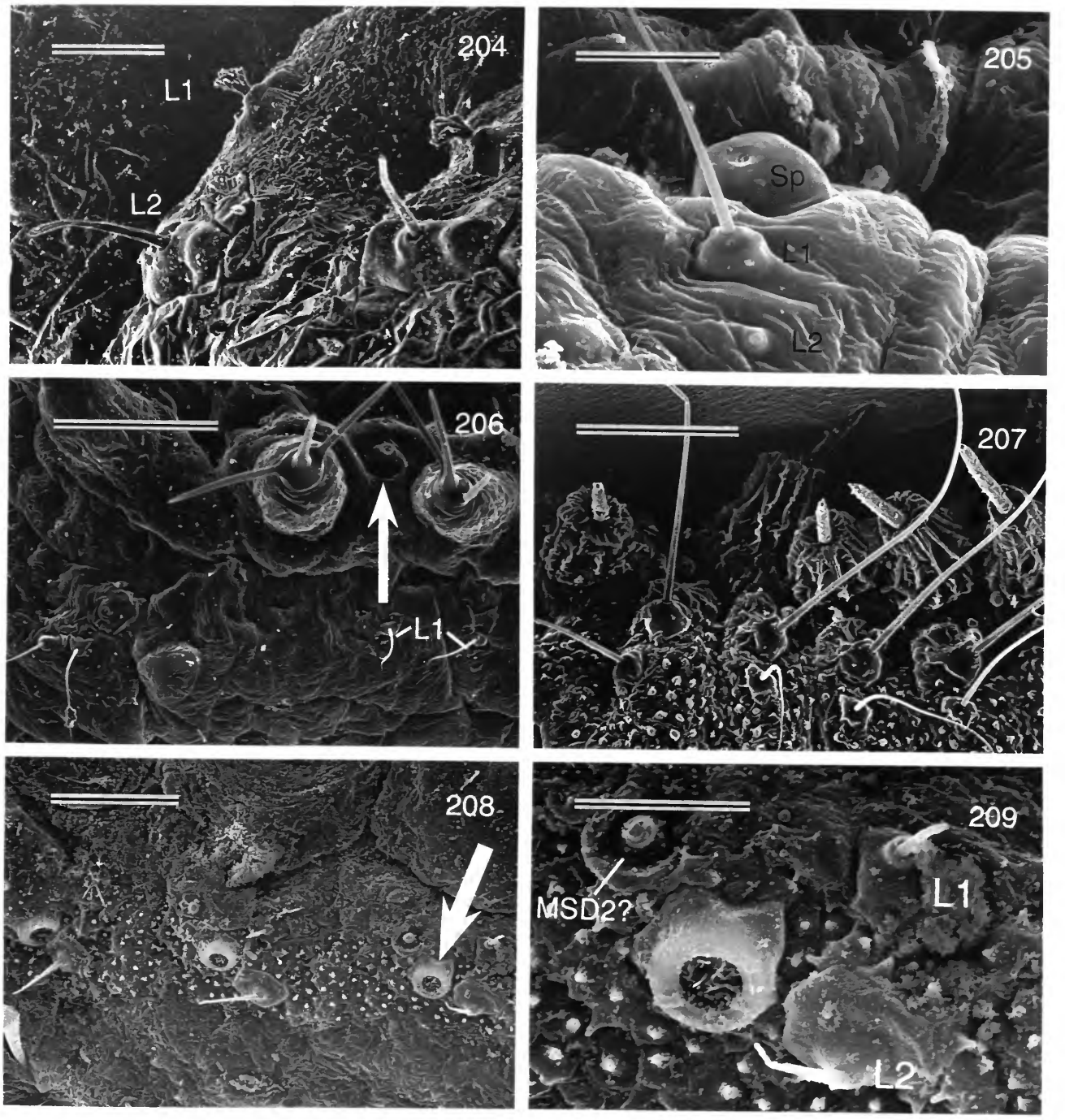
FIGURES 182–187.—Larval prothoracic setae in Limacodidae and Dalceridae (1st instar unless otherwise indicated; scale length in parentheses). 182, 183, *Semyra coarctata* complex: 182, prothoracic setae (100 µm); 183, L setae and spiracle (20 µm). 184, *Phobetron hipparchia* (50 µm); 185, *Crothaema* sp. (20 µm); 186, dalcerid sp., Ecuador (20 µm); 187, *Acraga infusa* complex (Dalceridae), late instar (note 3 L setae) (200 µm). (D, L, SD, XD = dorsal-, lateral-, subdorsal-, and X-dorsal-group setae, Sp = spiracle.)



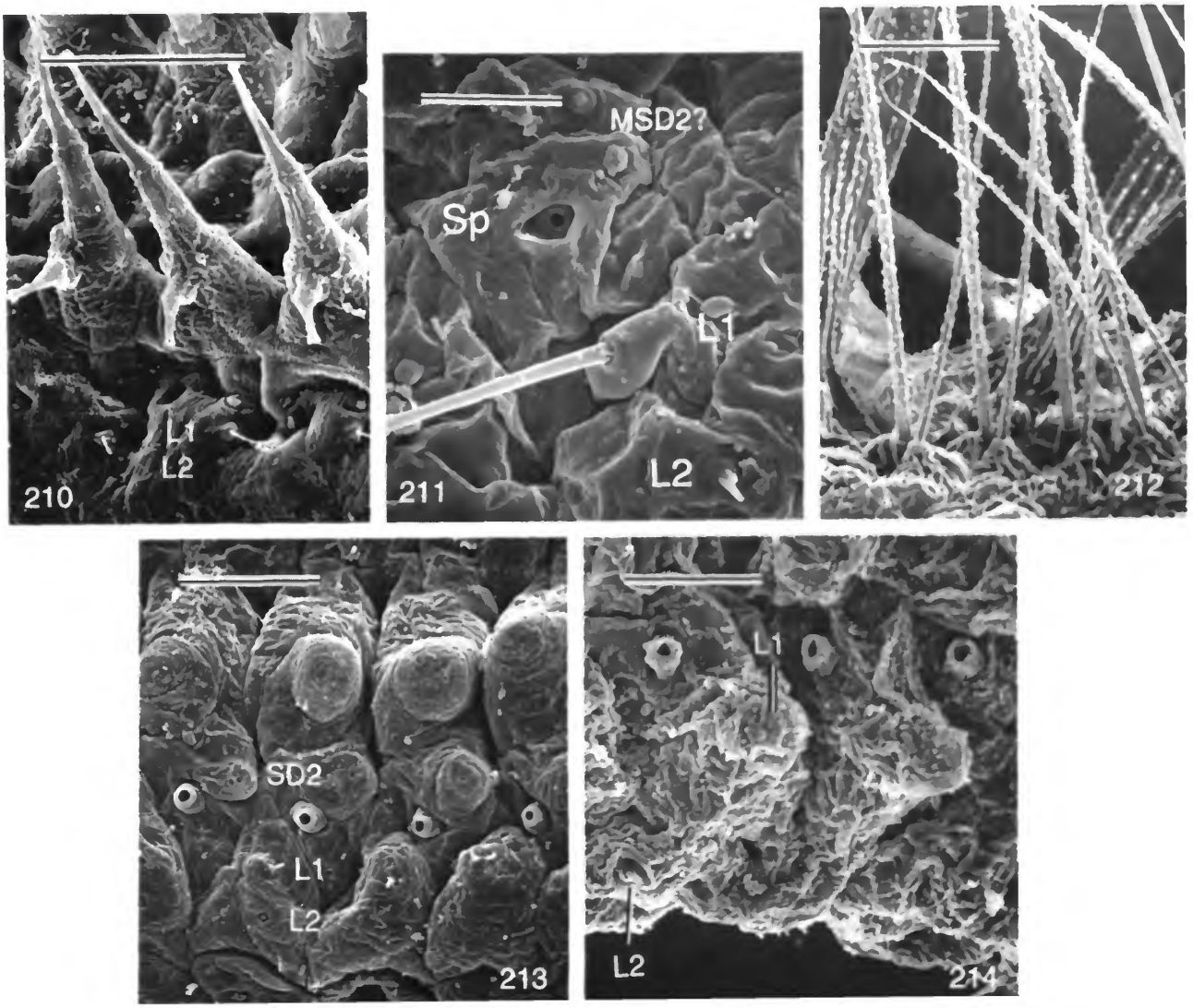
FIGURES 188–194.—Cuticular and gelatinous warts in 1st instars of Limacodidae and Dalceridae (scale length in parentheses). 188–190, *Belippa horrida:* 188, D and SD warts (100 μm); 189, detail of reduced seta on A3 wart (10 μm); 190, lateral view of setose wart on thorax (20 μm). 191, 192, *Pantoctaenia prasina:* 191, D and SD warts on A1–A7 (anterior to right) (100 μm); 192, detail of wart (20 μm). 193, 194, dalcerid sp., Ecuador: 193, D and SD rows A6–A9 (anterior to left) (100 μm); 194, detail of gelatinous wart (50 μm).



FIGURES 195–203.—Long tubercles in 1st instar Limacodidae (scale length in parentheses). 195–197, *Apoda biguttata:* 195, anterolateral view of D and SD tubercles (100 μm); 196, apex of SD tubercle prior to extension (5 μm); 197, apex of D tubercle (6 μm). 198–200, *Heuretes* sp.: 198, D tubercles (86 μm); 199, D and SD tubercles (SD are short, lateral setae to left) (43 μm); 200, SD tubercle (3.8 μm). 201–203, *Phobetron hipparchia:* 201, detail of partially extended tubercle (20 μm); 202, SD tubercles partially extended (50 μm); 203, tubercles fully extended (100 μm). (L, SD = lateral-, subdorsal-group setae or tubercles.)



FIGURES 204–209.—Abdominal setae proximate to spiracles in 1st instar Limacodidae and Dalceridae (scale length in parentheses): 204, *Semyra coarctata* complex (20 μm); 205, *Talima postica* (20 μm); 206, *Talima postica*, arrow points to "dorsal" spiracle on A1 between scoli on T3 (left) and A2 (100 μm); 207, *Phobetron hipparchia* (100 μm). 208, 209, dalcerid sp., Ecuador (anterior to left): 208, spiracular region (50 μm); 209, detail of setae and spiracle in 208 (see arrow) (20 μm). (L, MSD = lateral-, subdorsal-proprioceptor-group setae, Sp = spiracle.)



FIGURES 210–214.—Abdominal setae proximate to spiracles in 1st instar Limacodidae (scale length in parentheses): 210, *Euprosterna* sp. (100 μm); 211, *Apoda biguttata* (15 μm); 212, *Heuretes* sp. (50 μm); 213, *Pantoctaenia prasina* (75 μm); 214, *Crothaema* sp. (38 μm). (L, MSD, SD = lateral-, subdorsal-proprioceptor-, and subdorsal-group setae, Sp = spiracle.)

In dalcerids and in some limacodids, the L1 setae on T2 and T3 resemble D and SD setae or tubercles (Figures 177–181). SV setae on T2 and T3 occur dorsal to the legs in dalcerids (Figure 180) and in some limacodids (Figure 181). These are fungiform in first instar *Pantoctaenia* (Limacodidae) (see description of abdominal SV setae under "Ventral Surface of Body," below).

Dalcerids have a pair of proprioceptor setae on T2, MSD1 and MSD2, anteroventral to and near the gelatinous SD setae (Figure 180). There are three small setae proximate to each abdominal spiracle in dalcerids (Figures 180, 208, 209). I interpret the seta anterodorsal to the spiracle as MSD2 (fungiform in first instars) and the two posterior setae, one above the other, as L1 and L2. In zygaenids, Tremewan (1985) designated the MSD2 seta as SD2; however, MSD2 may be more appropriate for dalcerids because they often have two gelatinous D and SD setae in addition to the small seta (Figure 180). Singh and Goel (1987), and Miller (1991), noted that setae referred to as SD2 in noctuids and notodontids should be termed MSD2. Limacodids with two D and SD warts on the

abdomen appear to lack MSD setae on the abdomen (e.g., *Pantoctaenia*; Figures 181, 213); however, fungiform setae, proximodorsal to the spiracle, may be the MSD in *Apoda biguttata* (Figure 211).

Spiracles can vary in position; the Megalopygidae and Dalceridae, like Zygaenidae, have spiracles in roughly the same position on all abdominal segments, whereas in the Aididae and in some Limacodidae, the first abdominal spiracle is located more dorsally, supplanting the SD tubercle (Figure 206) (Dyar, 1899a:236).

Trosiines and megalopygines are unique in having either a digitate or a bulbous sensillum associated with each spiracle (Figures 168, 328–334). This has been referred to as a gland by Packard (1894) (see discussion of homology and function in "Megalopygidae" section, below).

VENTRAL SURFACE OF BODY.—The ventral surface of limacodid-group larvae is characterized either by the presence of prolegs on A2–A7, or by a slug-like surface bearing suckers (Figures 215–222, 223, 224). Thoracic legs are frequently reduced in the Zygaenoidea, especially in Limacodidae, Dalceridae, Epipyropidae, and Cyclotornidae. The tiny thoracic legs in first instar dalcerids and limacodids are roughly the size of the maxilla (Figures 112, 113).

The pretarsus of the thoracic legs has a similar shape in aidids, megalopygids, and somabrachyids (Figures 225–230). The claw projects horizontally from where it meets the round pretarsal base, and the claw apex extends past the base. In dalcerids and limacodids on the other hand, the claw is more curved and projects more vertically (Figures 231–233); as a result, the pretarsal base usually extends past the claw apex (Figures 231–233, 234–239). In aidids, megalopygids, and somabrachyids there is a globular seta on the inner margin of the pretarsus, at the base of the claw (Figures 225–230). Setae in this location have been referred to as axial setae in the Tineidae (Davis and Peña, 1990). In dalcerids and limacodids, the axial seta is hair-like (Figures 231, 232) or peg-like (Figure 233).

Thoracic leg setae, proximal to the pretarsus, can be either spatulate or hair-like and can either reach beyond the claw or be highly reduced (Figures 225–233). Spatulate setae appear in first or early instar megalopygids and in *Psycharium* (Figures 229, 230) and become more hair-like in later instars (Figure 228). In the Limacodidae the setae can be long and hair-like, extending past the claw, be reduced to fungiform either throughout the leg or on the coxae only (Figures 237–239), or be somewhat in-between as capitate setae (Figure 234, 273). The V1 seta of the thorax is hair-like in megalopygids (Figure 242), whereas it is fungiform in dalcerids (Figure 243) and in limacodids.

The cuticle texture of the sternum and of the coxae of the thoracic legs is shagreened in megalopygids and aidids but is smooth in dalcerids and limacodids (compared in Figures 240–245). There is a remnant of shagreened cuticle on the anteroventral portion of T1 in dalcerids (Figure 243).

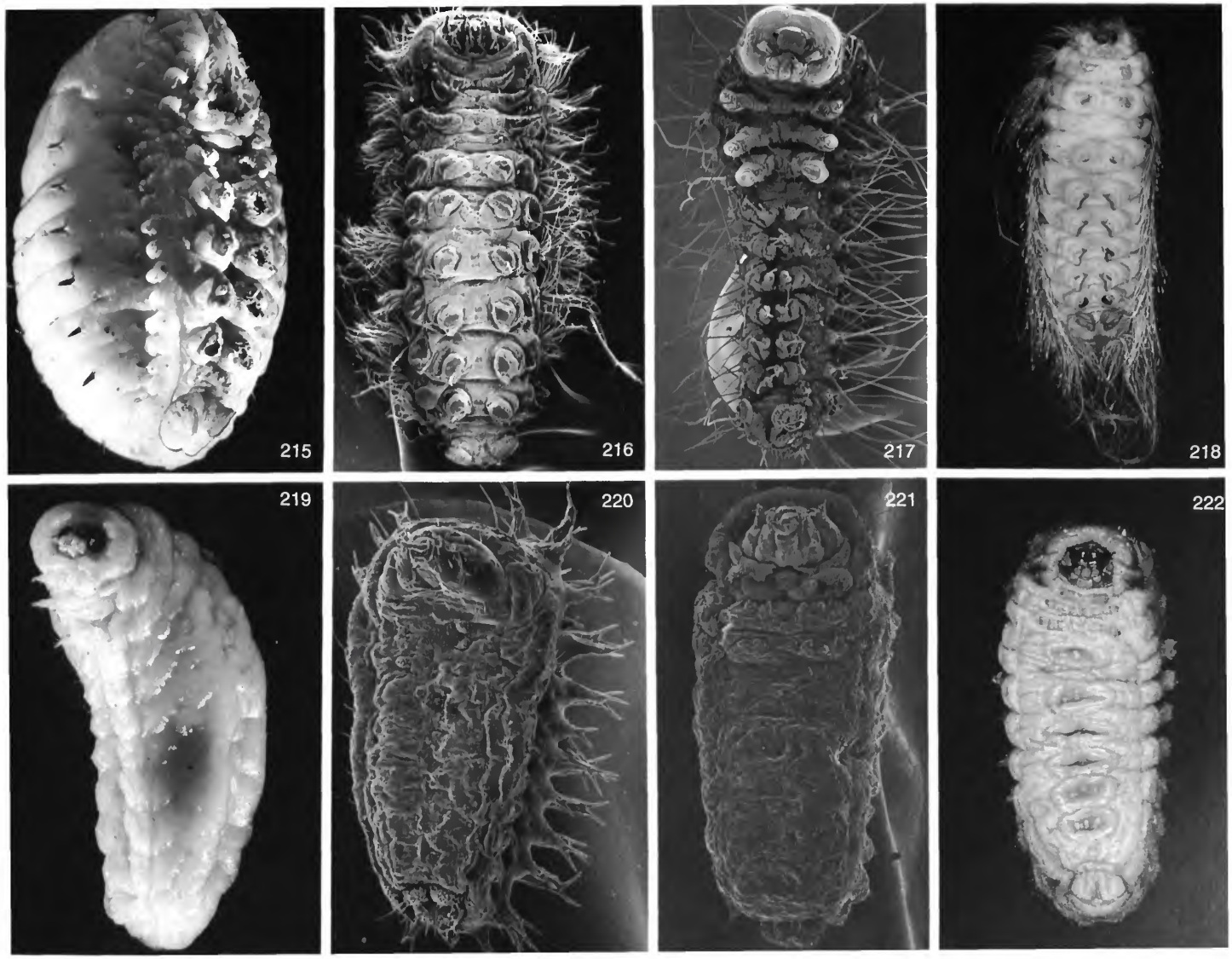
Prolegs in zygaenids (Figures 246–248) are more elongate and often have fewer crochets than do those of megalopygids, aidids, or somabrachyids. The Megalopygidae are widely reported to possess prolegs on A2 and A7 that lack crochets (Figures 254, 257). This condition also occurs in the Somabrachyidae (Figures 249, 250) (H. Geertsema, pers. comm.) and Aididae (Figure 223); however, some megalopygids have crochets on all prolegs (e.g., *Mesocia pusilla*) (Figures 216, 252, 253).

Megalopygid prolegs are unique among the Zygaenoidea in having membranous pads anterolateral to the crochets (Figures 252–257). The pads are absent on A10 and can be roughly equal in size on other segments or can be relatively large on the prolegs of A2 or A7 when crochets are absent. Similar pads occur in larvae of the Lycaenidae (Downey, 1987) and Riodinidae (Harvey, 1987), but in these families the pad interrupts the band of crochets.

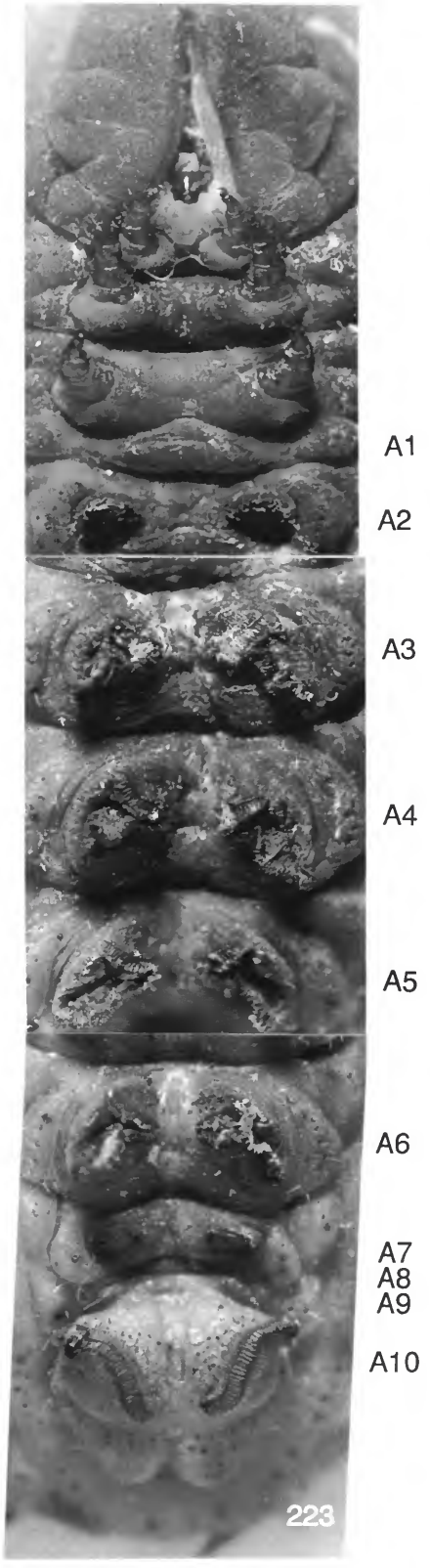
The presence of abdominal suckers in the Limacodidae (Chapman, 1894; Dyar, 1899b) and Dalceridae is unique in external-feeding lepidopteran larvae. Genera in these families have up to eight abdominal suckers, although the suckers on A1 and A8 are often feebly developed or absent (Figures 219, 222, 261, 266) (see "Homology of Suckers" for discussion).

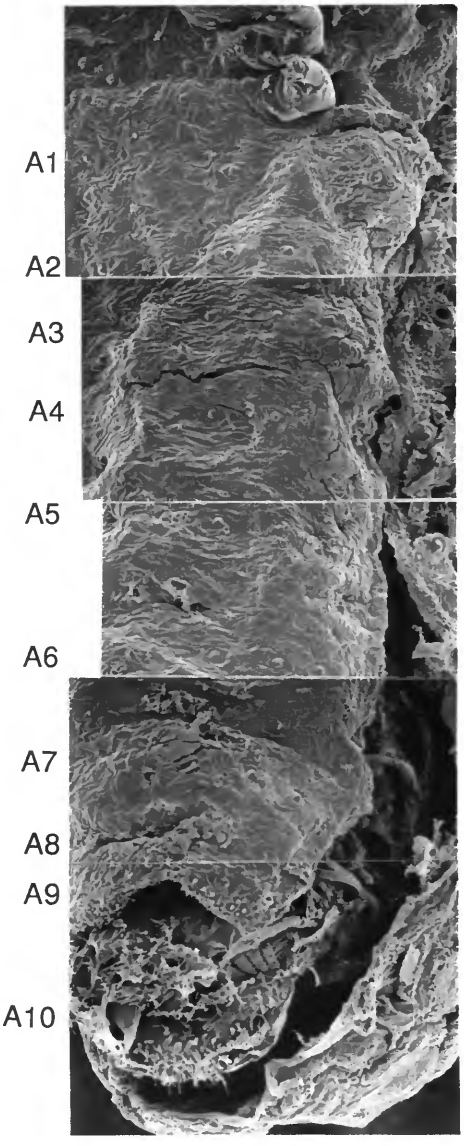
Late-instar larvae in the limacodid group exhibit a wide range in the number and a diversity of configurations of the uniordinal crochets on the A2–A7 prolegs. Late instar megalopygids have 20–70 crochets in linear or nonlinear rows, either divided by a distinct gap (e.g., *Norape*) or undivided (Figures 254, 256). Larval Aididae have 50–70 crochets that form a nearly continuous V-shaped row (Figures 340–344). Late instars of *Acraga infusa* (Dalceridae) have up to 17 crochets (Figure 264), five more than in *Dalcerides ingenita* (Stehr and McFarland, 1987). A *Megalopyge* sp. (Colombia, BMNH) has 12–14 crochets in the first instar (Figures 258, 259), an unusually large crochet number compared to early stage *Zygaena trifolii* and *Psycharium* sp., which each have four (Figures 248, 251). In the Somabrachyidae, late-instar larvae have crochets arranged in two separate rows. A *Somabrachys* sp. has up to 28 crochets (12 anterior, 16 posterior), and a *Psycharium* sp. has 18 crochets (five anterior, 13 posterior).

Larvae of the Dalceridae lack crochets in early instars (Figures 224, 262) but develop them on the A3–A6 prolegs by 4th instar (Figures 261, 263, 264). Additional crochets are sometimes added on A2 and A7, although fewer in number, in late instars (Stehr and McFarland, 1985, 1987). Crochets are reported as absent in the Limacodidae (Figures 222, 265–270) (Holloway, 1986; Stehr, 1987d); however, I found them to be present in *Pantoctaenia gemmans* (Figures 359, 360). *Pantoctaenia* develops crochets on A2–A7 and A10 (in roughly equal numbers) after the first instar, although the precise instar is not known.

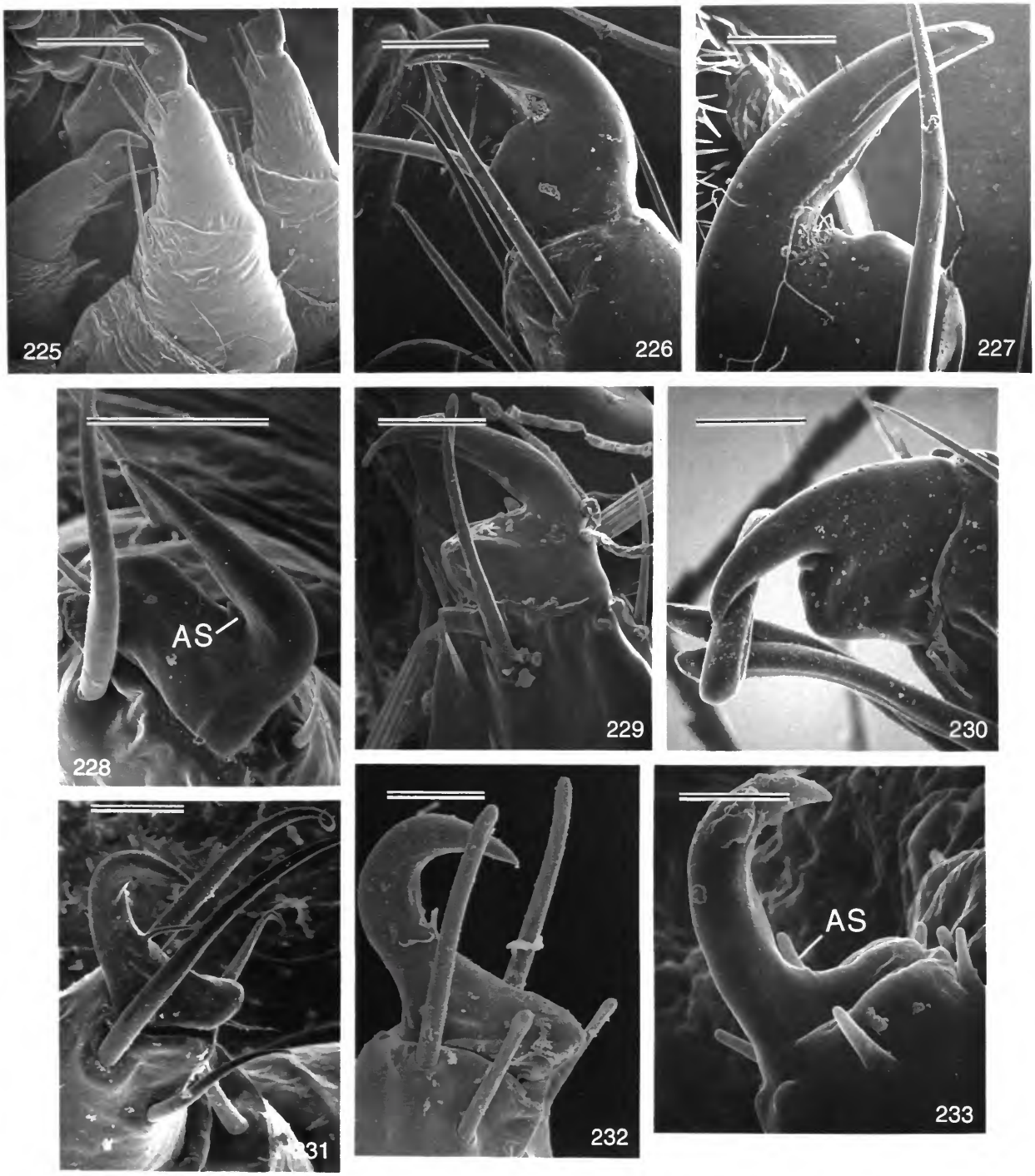


FIGURES 215–222.—Larval habitus in ventral view (post-first instar unless otherwise indicated): 215, *Aidos* sp. (Aididae) (photo by C. Hansen); 216, *Mesocia pusilla* (Trosiinae); 217, *Psycharium* sp. (Somabrachyidae) (1st instar); 218, *Megalopyge lanata* (Megalopyginae) (photo by L. Minor-Penland); 219, *Pantoctaenia gemmans* (Limacodidae) (photo by C. Hansen); 220, *Semyra coarctata* complex (Limacodidae) (1st instar); 221, *Euprosterna* sp. (Limacodidae) (1st instar); 222, *Acharia* sp. (Limacodidae) (photo by L. Minor-Penland).

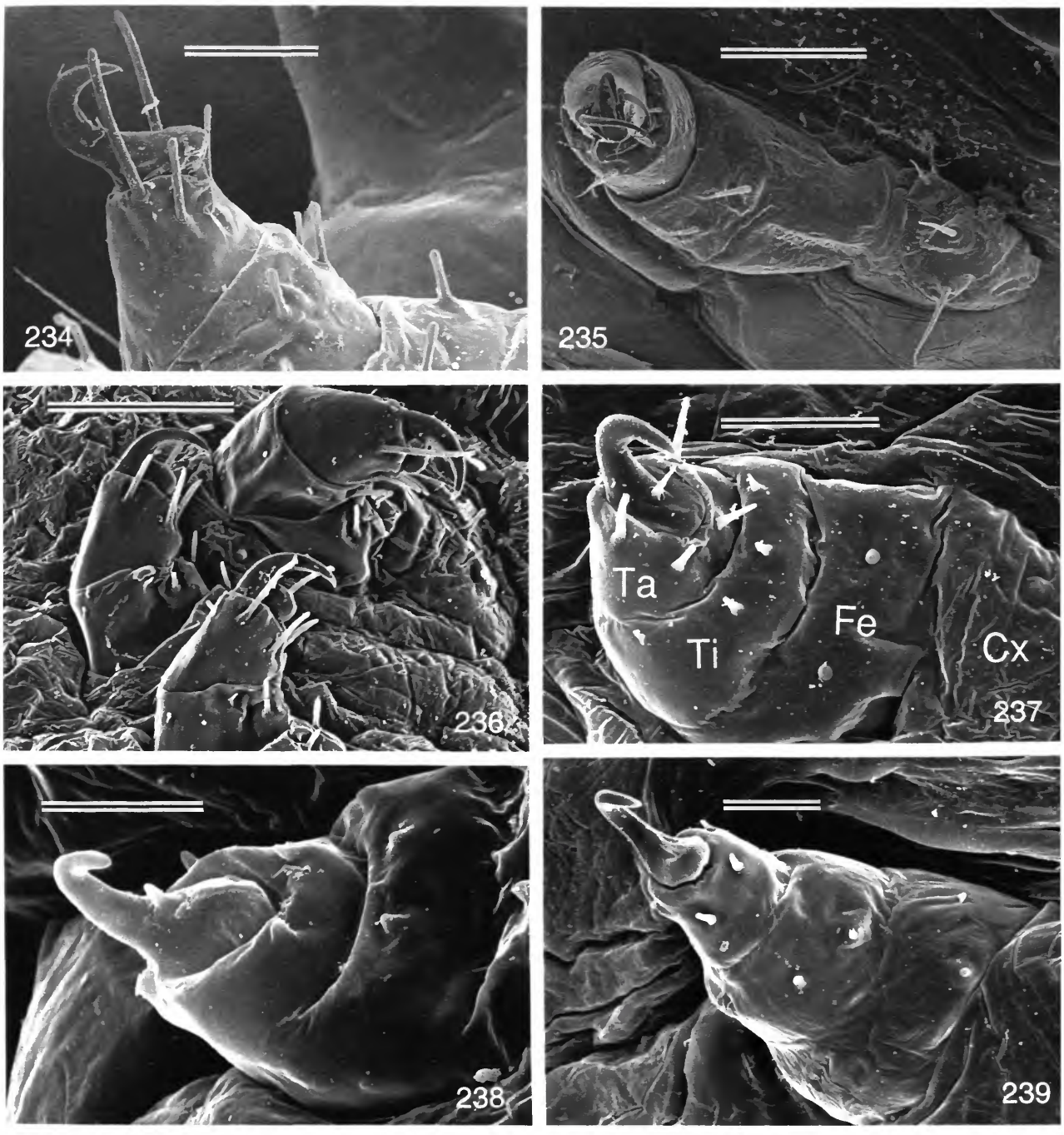




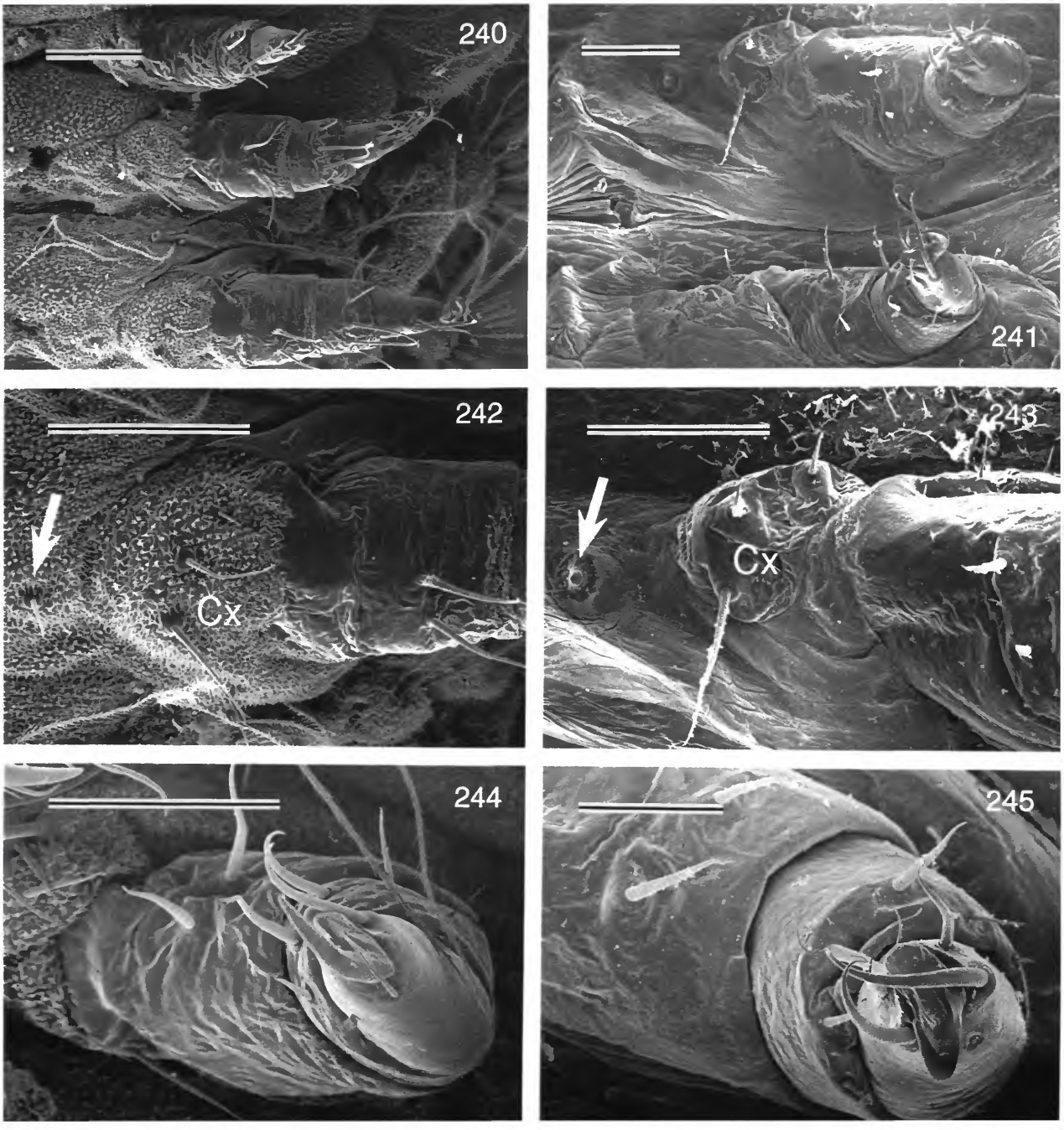
FIGURES 223, 224.—Detail of larval ventrum: 223, *Aidos* sp. (Aididae), Venezuela (late instar) (photo by L. Minor-Penland); 224, dalcerid sp., Ecuador (1st instar). (A1–A10 = abdominal segments 1–10.)



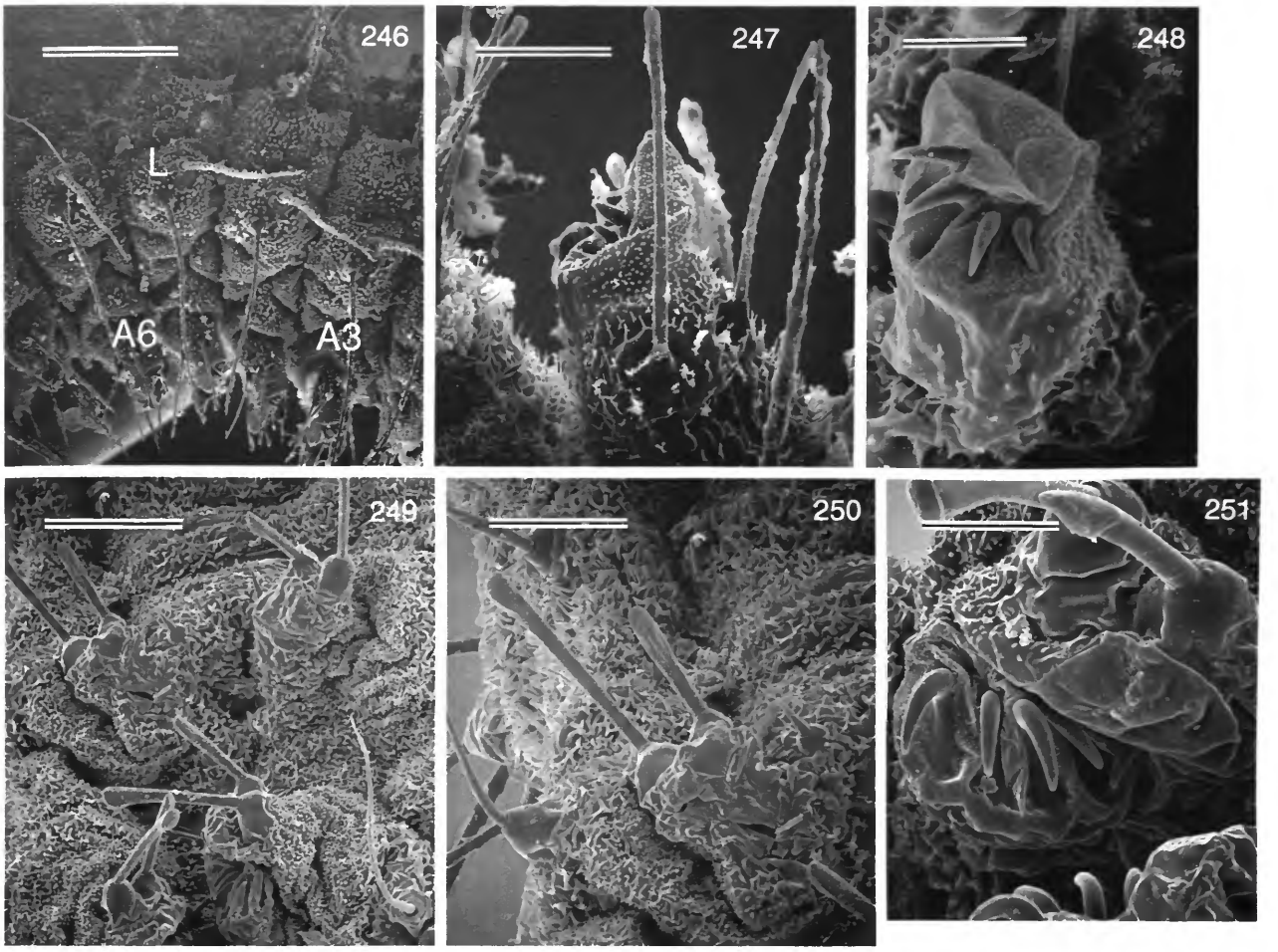
FIGURES 225–233.—Larval thoracic legs and pretarsal claw in the limacodid group (scale length in parentheses). 225–227, *Aidos* sp. (Aididae), from exuvia of ultimate instar: 225, thoracic legs (0.38 mm); 226, detail of 225 (120 μm); 227, detail of claw (75 μm). 228, *Mesocia pusilla* (Trosiinae) (50 μm); 229, *Megalopyge* sp. (Megalopyginae), 1st instar (20 μm); 230, *Psycharium* (Somabrachyidae), 1st instar (15 μm); 231, *Acraga infusa* complex (Dalceridae), middle instar (50 μm); 232, *Semyra coarctata* complex (Limacodidae), 3rd instar (20 μm); 233, *Apoda biguttata* (Limacodidae), 1st instar (4.3 μm). (AS = axial seta.)



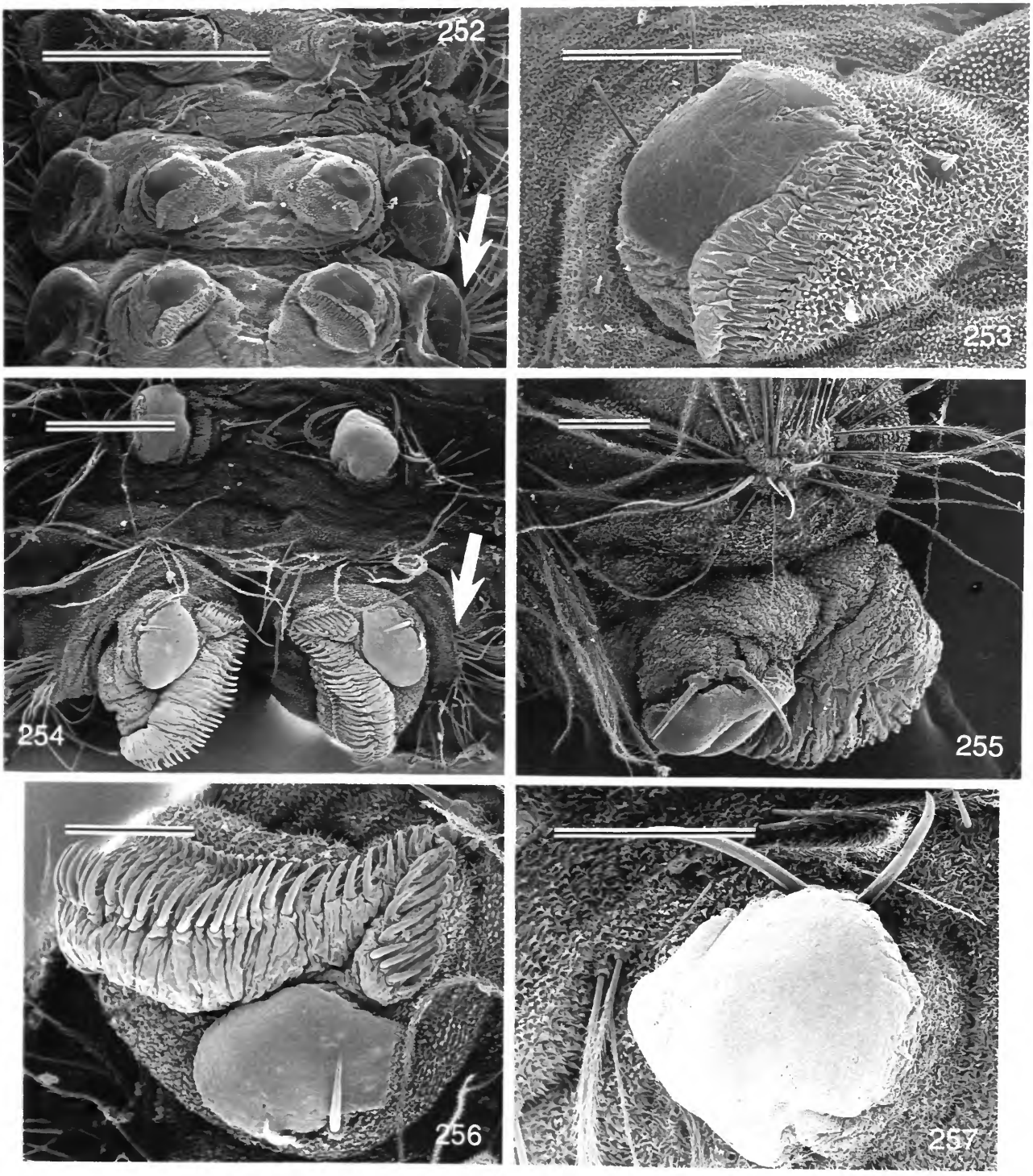
FIGURES 234–239.—Larval thoracic legs in Limacodidae and Dalceridae (scale length in parentheses): 234, *Semyra coarctata* complex, 3rd instar (50 μm); 235, *Acraga infusa* complex (Dalceridae), middle instar (200 μm); 236, *Pantoctaenia*, legs on T1–T3, 1st instar (50 μm); 237, *Phobetron hipparchia*, 1st instar (20 μm); 238, *Talima postica*, 1st instar (10 μm); 239, *Natada subpectinata*, post-first instar (20 μm). (Cx = coxa, Fe = femur, Ta = tarsus, Ti = tibia.)



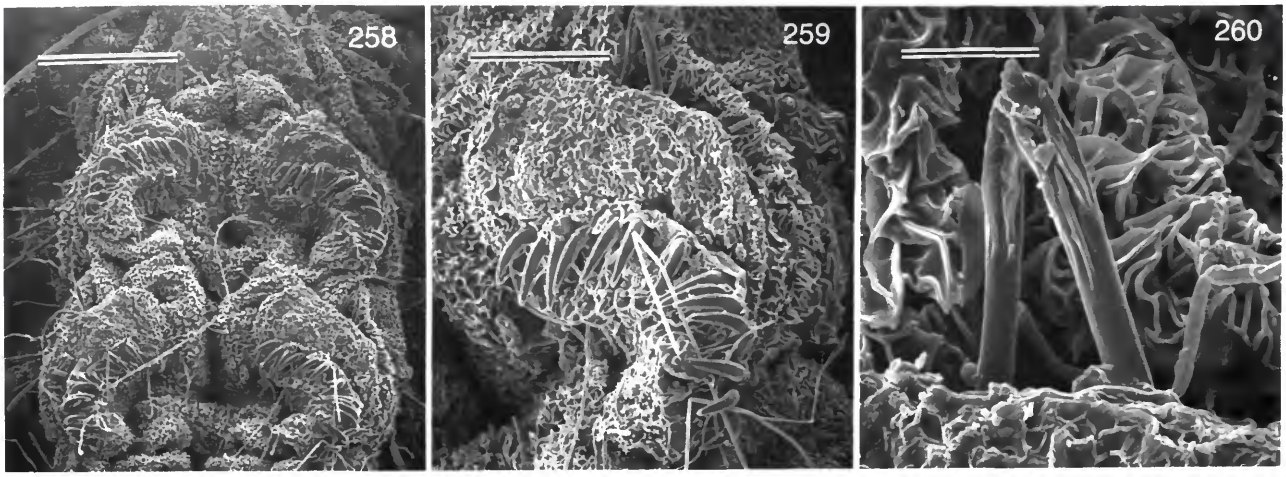
FIGURES 240–245.—Comparison of thoracic ventral skin texture and setae between middle instar Megalopygidae (left) and Dalceridae (right) (scale length in parentheses). 240, 242, 244, *Mesocia pusilla* (Megalopygidae): 240, entire legs, T1–T3, and shagreened cuticle at base (200 µm); 242, base of 1 leg (arrow points to homologous V1 seta found in *Acraga*, to right) (200 µm); 244, detail of 1 leg (200 µm). 241, 243, 245, *Acraga infusa* complex (Dalceridae): 241, entire legs, T1 and T2 (200 µm); 243, base of 1 leg (arrow points to homologous V1 seta, found to left; note shagreened cuticle above) (200 µm); 245, detail of 1 leg (100 µm). (Cx = coxa.)



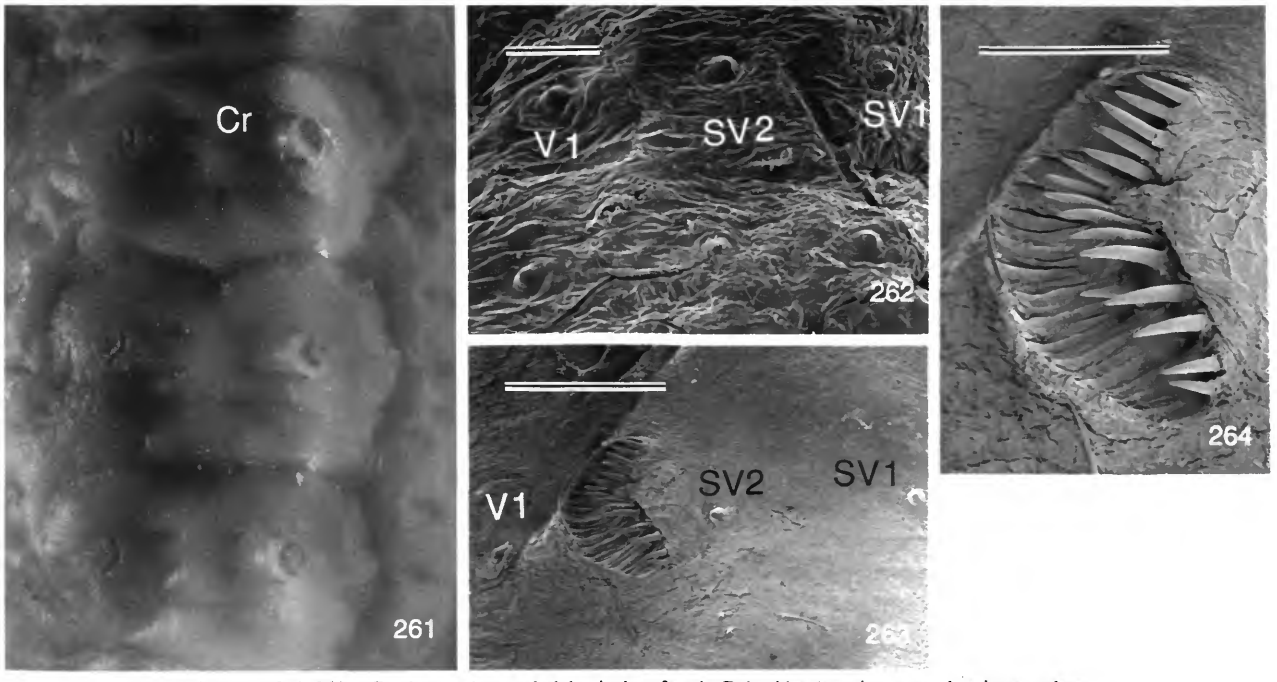
FIGURES 246–251.—Prolegs in 1st instar Zygaenidae and Somabrachyidae (scale length in parentheses). 246–248, *Zygaena trifolii:* 246, lateral view of prolegs A3–A6 (136 µm); 247, lateral view of A4 (30 µm); 248, proleg A5, viewed from below (20 µm). 249–251, *Psycharium* sp. (Somabrachyidae): 249, proleg pairs on A2 (above) and A3 (75 µm); 250, detail of proleg A2 (50 µm); 251, detail of proleg A4 (27 µm). (A3, A6 = abdominal segments 3,6, L = lateral-group setae.)



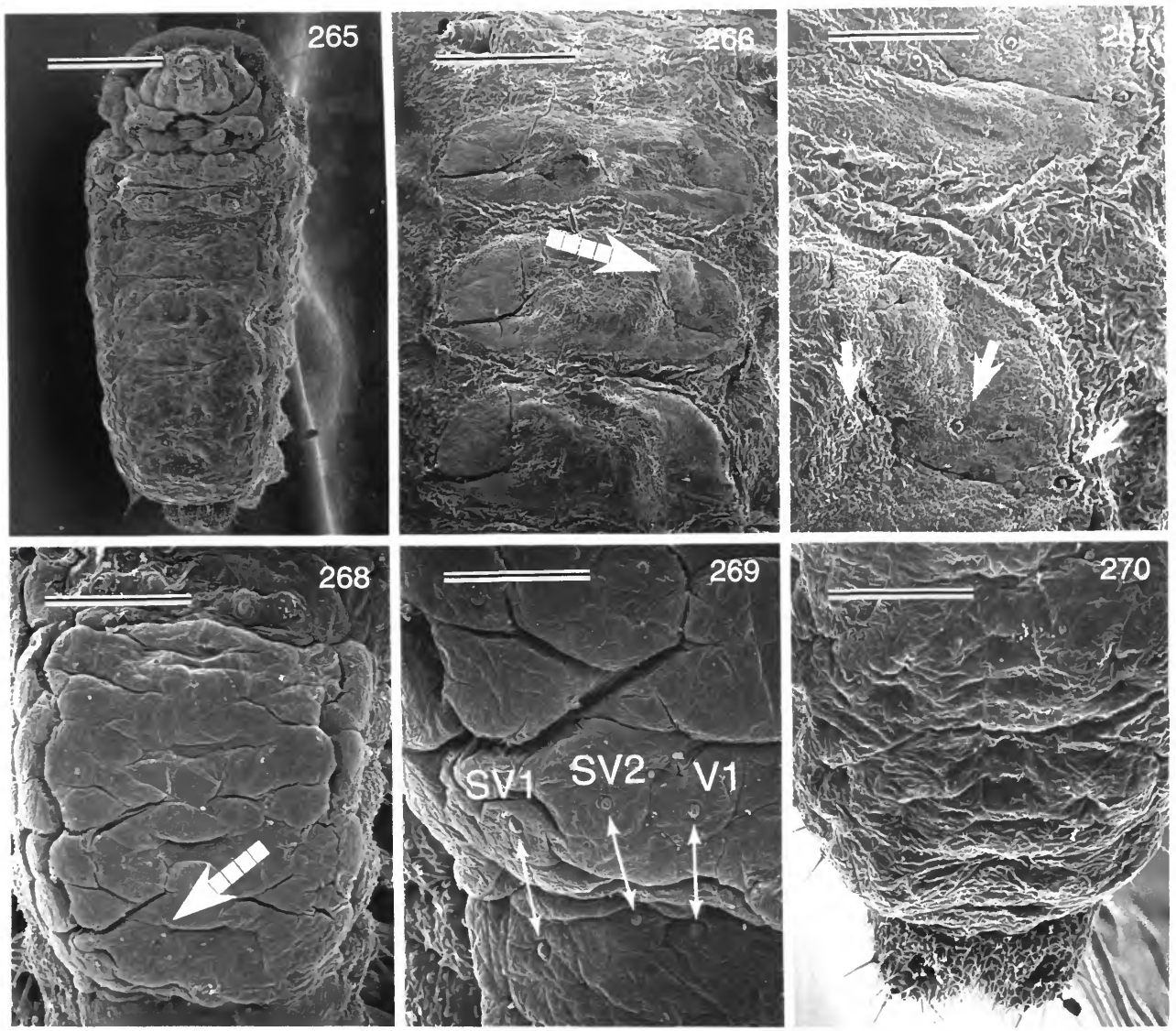
FIGURES 252–257.—Prolegs in Megalopygidae (scale length in parentheses). 252, 253, *Mesocia pusilla* (Trosiinae): 252, prolegs A2 and A3 (arrow points to additional membranous pad on SV verruca) (1 mm); 253, detail of A2 proleg (200 µm). 254–257, *Megalopyge crispata* (Megalopyginae): 254, prolegs A2 and A3 (arrow points to normal SV verrucae) (500 µm); 255, proleg A3, lateral aspect (200 µm); 256, detail of A3 proleg (200 µm); 257, detail of A2 proleg (200 µm).



FIGURES 258–260.—Prolegs of 1st instar Megalopygidae (*Megalopyge* sp.) (scale length in parentheses): 258, prolegs A2–A4 (120 μm); 259, detail of A4 proleg (50 μm); 260, detail of A4 subventral setae located at top of 259 (12 μm).

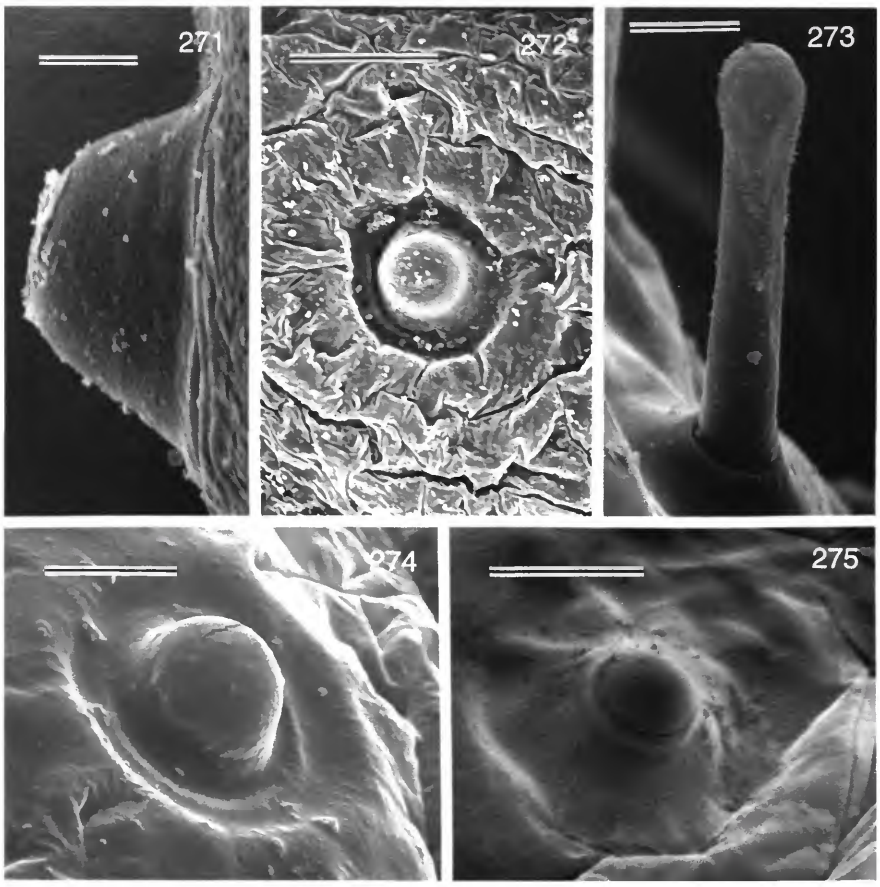


FIGURES 261–264.—Crochets and ventral abdominal surface in Dalceridae (anterior at top, late instar unless otherwise indicated; scale length in parentheses): 261, crochets on segments A3–A5, *Dalcerina tijucana* (photo by L. Minor-Penland); 262, detail of ventral surface and fungiform setae, 1st instar dalcerid species, Ecuador (meson to left) (20 μm). 263, 264, *Acraga infusa* complex: 263, crochets in relation to homologous setae in 262 (meson to left) (200 μm); 264, detail of crochets (100 μm). (Cr = crochets, SV, V = subventral-, ventral-group fungiform setae.)



FIGURES 265–270.—Ventral abdominal surface of Limacodidae (anterior at top, 1st instar unless otherwise indicated; scale length in parentheses): 265, *Belippa horrida* (200 μm). 266, 267, *Semyra coarctata* complex, 4th instar (200 μm): 266, suckers on A2–A4 (500 μm); 267, detail of 266 (see arrow), arrows point to fungiform setae homologous to those of Dalceridae in 262, 263 (200 μm). 268, 269, *Phobetron hipparchia:* 268, ventrally extended segments A1–A5 (150 μm); 269, detail of 268 (see arrow), arrows point to fungiform setae SV1, SV2, V1 (60 μm). 270, *Pantoctaenia prasina,* posterior segments (note shagreened texture of A10 at bottom vs. smooth segments above) (86 μm).

The crochets on the A10 proleg are a linear undivided mesoseries in the Megalopygidae (Figures 278, 284), Aididae (Figure 223), and Zygaenidae, although they are semicircular in first instar *Psycharium* and *Zygaena trifolii* (Figures 281, 283). Crochets on A10 are absent in dalcerids and limacodids except in post-first instar *Pantoctaenia* (Figure 360).

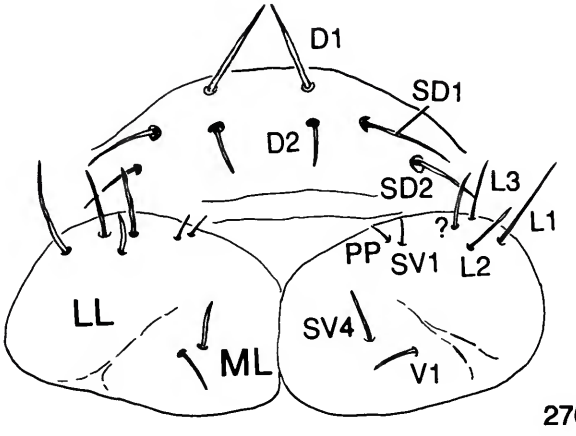


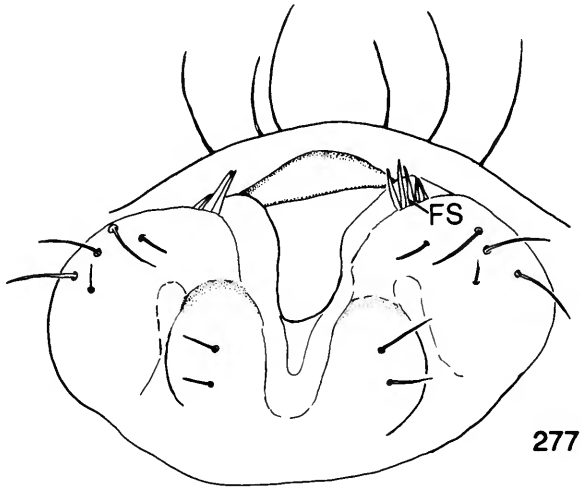
FIGURES 271–275.—Modified larval setae on ventral surface and thoracic legs in Dalceridae and Limacodidae (scale length in parentheses): 271, *Acraga infusa* complex (Dalceridae), lateral view of fungiform seta (5 μm). 272, 273, *Semyra coarctata* complex: 272, abdominal seta (20 μm); 273, capitate seta on leg (5 μm). 274, *Acharia stimulea*, abdominal seta (10 μm); 275, *Acraga infusa* complex, abdominal seta (20 μm).

First instar *Zygaena trifolii* (Figure 247), *Psycharium* (Figure 249–251), and megalopygids (Figure 260) have two spatulate SV setae on the anterior portion of the prolegs. These are hair-like in later instars except in *Psycharium*, in which they become spines and increase in number.

Fungiform SV and V setae are present on the ventral portions of the abdomen on A1–A9 in larval limacodids and dalcerids (Figures 224, 271, 272, 274, 275). The most dorsal of these fungiform setae is SV1, with SV2 and V1 located towards the meson (Figures 180, 181, 262, 263). SV and V setae were previously unreported in limacodids and were considered absent in dalcerids (Stehr and McFarland, 1987); however, they are present from first to final instar in each family, and crochets develop between SV2 and V1 setae in later instar dalcerids and in *Pantoctaenia* (Figures 262, 263).

Stehr (1987a:455) reported that the dorsum of A10, or anal plate, in megalopygid caterpillars is reduced to "a small lobe" that is "tucked beneath" the dorsum of A9. Viewed from above, this gives A9 the appearance of being "the terminal segment." Adding to this impression is the location of the A10 proleg, directly below the dorsum of A9. The ventral portion of A9 is very narrow and forms a functional segment with A8 above and below. In effect, the ventrum of segment A9 and of A10 has a functional counterpart on the dorsum one segment removed to the anterior. Although reported only in Megalopygidae, this condition occurs throughout the limacodid group but to a lesser





FIGURES 276, 277.—Chaetotaxy of anal segment (A10) in Dalceridae and Limacodidae (late instars): 276, *Acraga infusa* complex (Dalceridae); 277, *Phobetron hipparchia*. (D, L, SD, SV, V = dorsal-, lateral-, subdorsal-, subventral-, and ventral-group setae, FS = frass-flipping setae, LL = lateral lobe, ML = mesal lobe, PP = paraproct seta.)

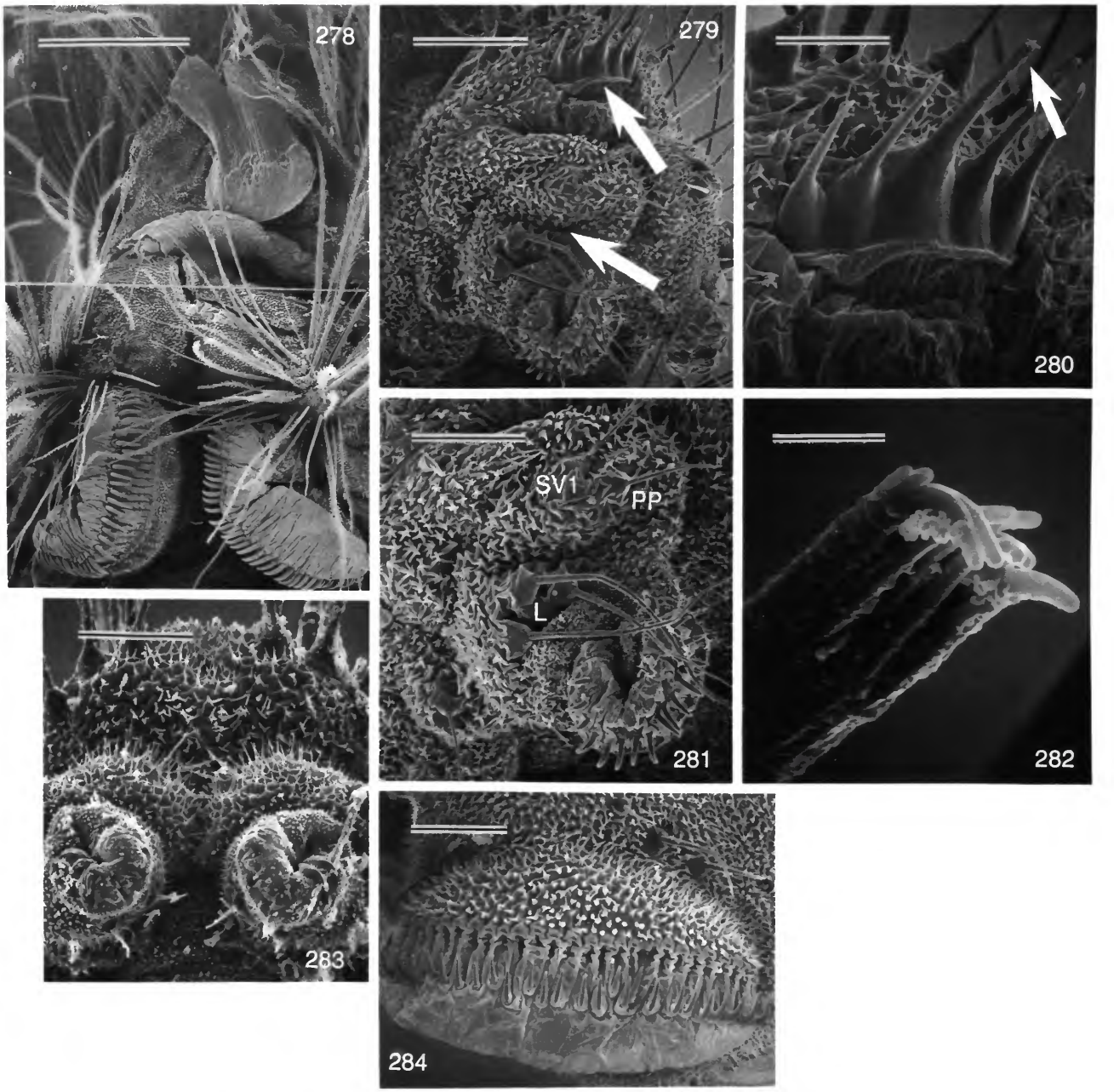
degree in the Somabrachyidae. The anal plate in most of the limacodid group bears either pairs only of primary D and SD setae (Figures 276, 277) or a narrow row that includes secondary setae, compared to an anal plate with verrucae in late instar Zygaenidae and Somabrachyidae.

An anal fork or anal comb used for frass removal is located between the anal plate and the anus. It is present in the Megalopygidae (Figure 278) and Somabrachyidae (Jordan, 1909) (Figures 279, 280, 282) and is present or absent (Figure 283) in the Zygaenidae and Aididae. I use the term anal fork for a single medial process with a emarginate dorsal border (Figure 278) and the term anal comb for a row of stout spines (Figures 279, 280). Neither is present in the Limacodidae and Dalceridae (Figures 276, 277, 285–287, 293–296), although nonhomologous setae of similar function sometimes occur below the anus (see next paragraph).

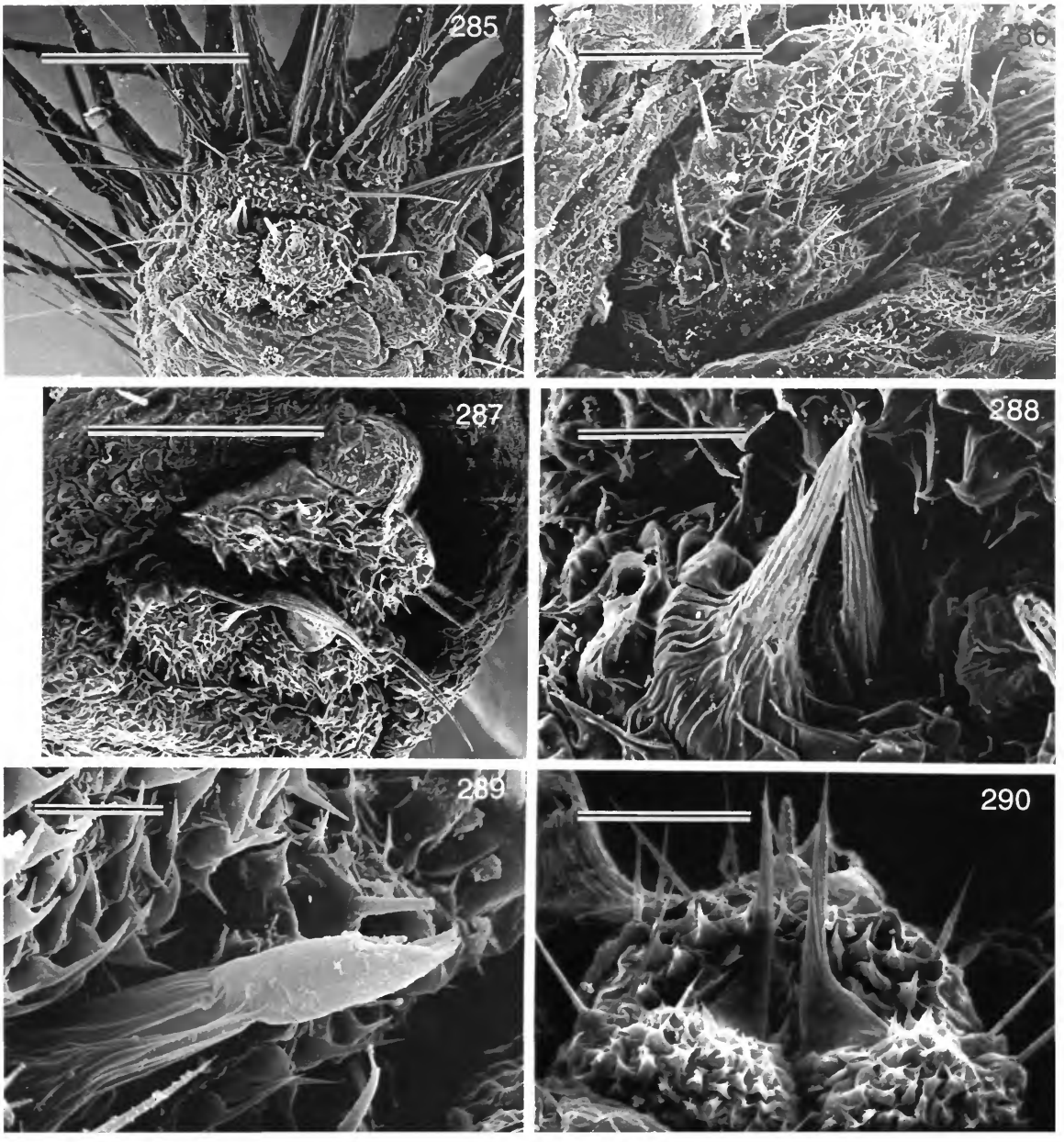
Prolegs on A10 in the Dalceridae (Stehr and McFarland, 1987) and Limacodidae consist of two small spinulose lobes (Figures 276, 277). The lateral lobe has five or six stout setae on each side, and the smaller mesal lobe has two. In middle to late instars, the outer portion of the lateral lobe consists of three L setae and either one secondary or one SV seta; the one or two setae near the meson are either paraproct setae or SV1 setae (Stehr, 1987b). The two setae of the mesal lobe represent either SV4 and V1 setae anterior to the proleg base in other Lepidoptera (Stehr, 1987b) or any of the SV1–SV3 setae (Figure 276). In either case this would be a reduction from the condition in *Zygaena trifolii* (Tremewan, 1985). Wider, peg-like setae on the dorsomesal margin of the lateral lobe are used for flipping frass (Stehr and McFarland, 1987). These setae occur in dalcerids (Figures 286, 289) and limacodids (Figures 277, 287, 288, 290), although they can be absent in either family (Figures 276, 293, 295, 296). Crochets in late-instar *Pantoctaenia* (Limacodidae) develop between the lateral and mesal lobes of A10 (Figures 360, 361).

PUPAE

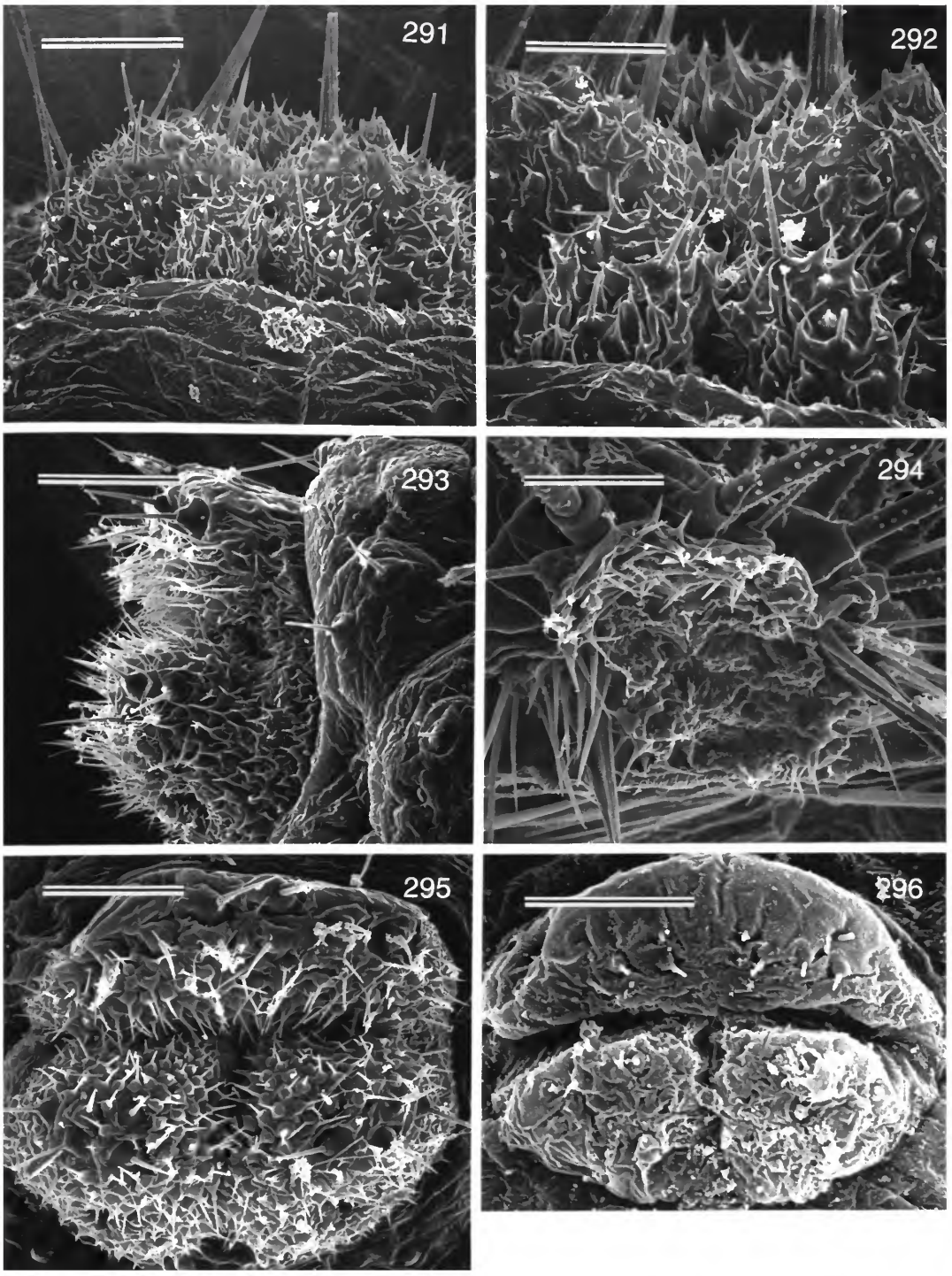
Several pupal character states in the Zygaenidae and in the limacodid group have led past workers to consider them primitive. These include (1) thin cuticle; (2) moveable abdominal segments A3–A6; (3) eclosion outside the cocoon; and (4) visible A1 spiracles. The last, however, may be a synapomorphy for the Zygaenoidea because it does not occur in lower ditrysian superfamilies, such as Tineoidea (D.R. Davis, pers. comm.). The presence of an exposed spiracle on A1 was noted by Mosher (1916) as a character state shared by the Zygaenidae (as Pyromorphidae), Limacodidae (as Eucleidae), and Megalopygidae. The spiracle also is visible in the Cyclotornidae (Common, 1990), whereas it is either hidden (Common, 1990) or visible in the Epipyropidae (discussed further in the section on Epipyropidae, below).



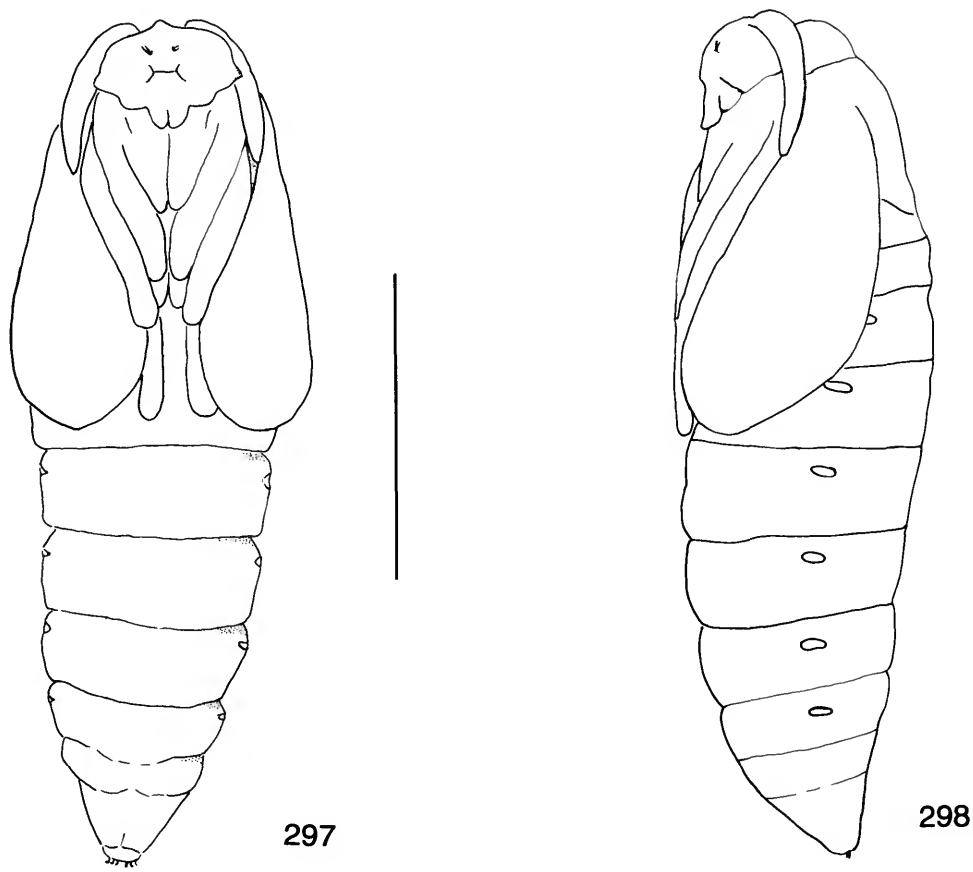
FIGURES 278–284.—Anal segment (A10) in Megalopygidae, Zygaenidae, and Somabrachyidae (scale length in parentheses): 278, anal fork and prolegs of *Megalopyge crispata* (Megalopyginae), late instar (500 μm). 279–282, *Psycharium* sp. (Somabrachyidae), 1st instar: 279, anal comb (upper arrow) and prolegs (lower arrow) (111 μm); 280, detail of anal comb, arrow points to middle prong (40 μm); 281, detail of anal proleg (75 μm); 282, detail of middle prong of anal comb in 280 (see arrow) (3 μm). 283, anal prolegs and plate of *Zygaena trifolii* (Zygaenidae) (60 μm); 284, anal proleg of *Mesocia pusilla* (Trosiinae) (100 μm). (L, SV = lateral-, subventral-group setae, PP = paraproct seta.)



FIGURES 285–290.—Anal segment (A10) in 1st instar Limacodidae and Dalceridae (scale length in parentheses): 285, posteroventral aspect of *Phobetron hipparchia* (200 µm). 286, 287, posterolateral aspect of anal plate and vestigial proleg: 286, *Dalcerides ingenita* (Dalceridae) (100 µm); 287, *Semyra coarctata* complex (100 µm). 288, 289, detail of frass-flipping setae: 288, *Phobetron hipparchia*, detail of 285 (20 µm); 289, *D. ingenita* (Dalceridae) (20 µm). 290, ventral aspect of *Semyra coarctata* complex (50 µm).



FIGURES 291–296.—Anal segment (A10) in 1st instar Limacodidae and Dalceridae (scale length in parentheses). 291, 292, ventral view of anal proleg of *Phobetron hipparchia:* 291, contrast between smooth A9 and spinulose A10 (50 μm); 292, detail of spinulose A10 in 291 (27 μm). 293, lateral view of anal proleg and plate of *Pantoctaenia gemmans* (50 μm). 294–296, posterior view of anal segment: 294, *Heuretes* sp. (27 μm); 295, *P. gemmans* (50 μm); 296, *Euprosterna* sp. (50 μm).



FIGURES 297, 298.—Pupa of Dalceridae (*Acraga infusa* complex) (scale = 5 mm): 297, ventral aspect; 298, lateral aspect.

Minet (1986) considered an A2 spiracle that is covered by the hindwing to be a synapomorphy for the Zygaenoidea. In limacodid (Common, 1990) and megalopygid pupae, however, spiracles on both A1 and A2 are visible. Only the A2 spiracle is visible in dalcerid pupae (Figures 297, 298). Pupal spiracles in the Megalopygidae (Figure 302) are unique in having lobes (Mosher, 1916) and are similar in shape and position to those found in the larvae (Figures 328–334), but they occur on fewer segments (e.g., *Megalopyge lanata*, A1–A6 in females, A1 only in males).

The pupal eyepiece in the limacodid group has a lateral extension called the sculptured flange (Chapman, 1894:349; Mosher, 1916) (Figures 303, 307). Reported as a potential synapomorphy for Limacodidae + Megalopygidae (Holloway, 1986), it also occurs in the Dalceridae (Figure 303) (Epstein, 1988) and Aididae. The sculptured flange, located over the T2 spiracle, moves up and down during respiratory ventilation in megalopygid pupae (Mosher, 1916). Following eclosion, this structure either remains attached (Figures 303, 315, 317) or dehisces (Figures 304, 312–314, 316, 318, 319) from the head capsule.

As is the adult proboscis, the pupal proboscis in the limacodid group is weakly developed compared to the Zygaenidae. A lateral lobe connected to the maxilla, found in some lineages of Limacodidae (+ Chrysopolomidae) (Figures 316, 317), has been termed the "maxillary palpus" or "eye collar" (Chapman, 1893:115), "lateral process connected with it [the maxillary palpus]" (Packard, 1895a:797), and the

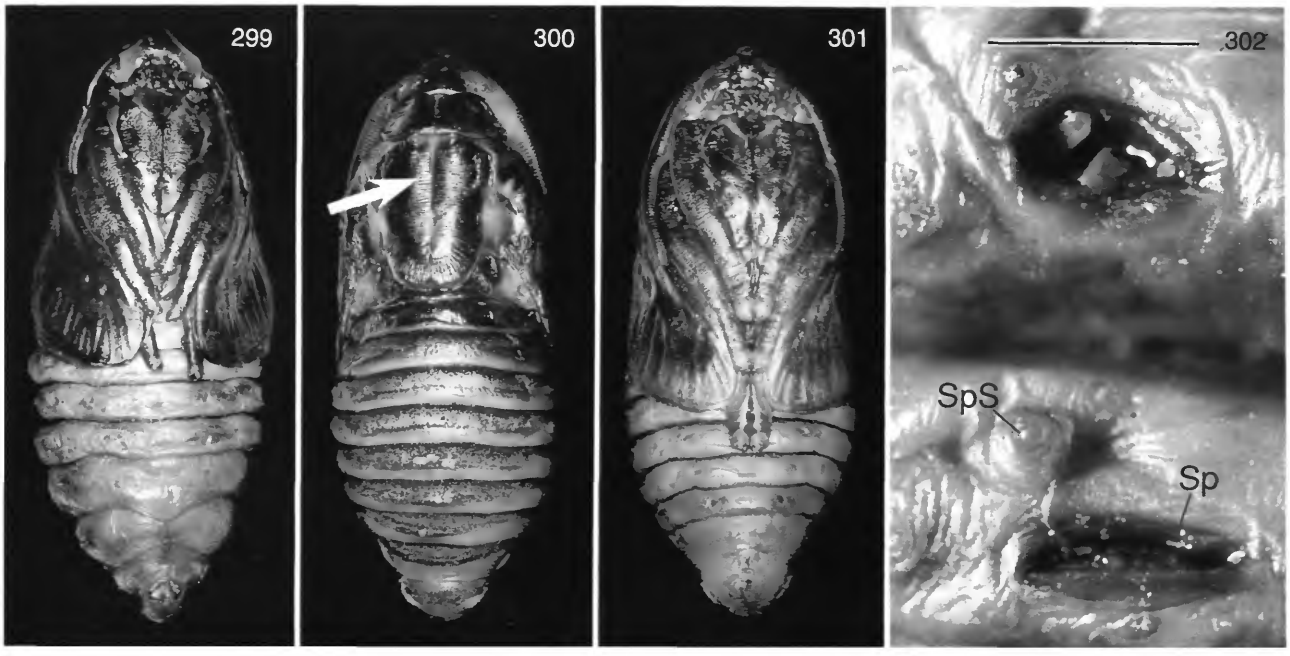
"lateral prolongation [of the maxilla]" (Mosher, 1916:43). I refer to it as the maxillary extension. This structure may function to hold the free front legs of "incomplete" pupae in place at the femur-tibia joint, along with the sculptured eye flange and antenna. Loss of the maxillary extension is likely to have occurred independently within several lineages of New World Limacodidae with spiny larvae (Figures 318, 319). A similar maxillary structure occurs in the Nepticuloidea (Chapman, 1893), including Opostegidae (Davis, 1989).

The pupal frons, which commonly projects as a rounded bump (Figure 320), may assist in forcing open the cocoon in megalopygids. In dalcerids, the frons can have up to six (in two groups of three) closely appressed setae (e.g., *Dalcerides ingenita*) (Figure 325). The frons may be rough and shagreened in limacodids, perhaps to assist with weakening or freeing the lid (e.g., *Phobetron pithecium,* Limacodidae) (Figures 322–324). The nonmovable pupal mandibles in species of the limacodid group are usually distinguishable from the frontoclypeus (Figure 321).

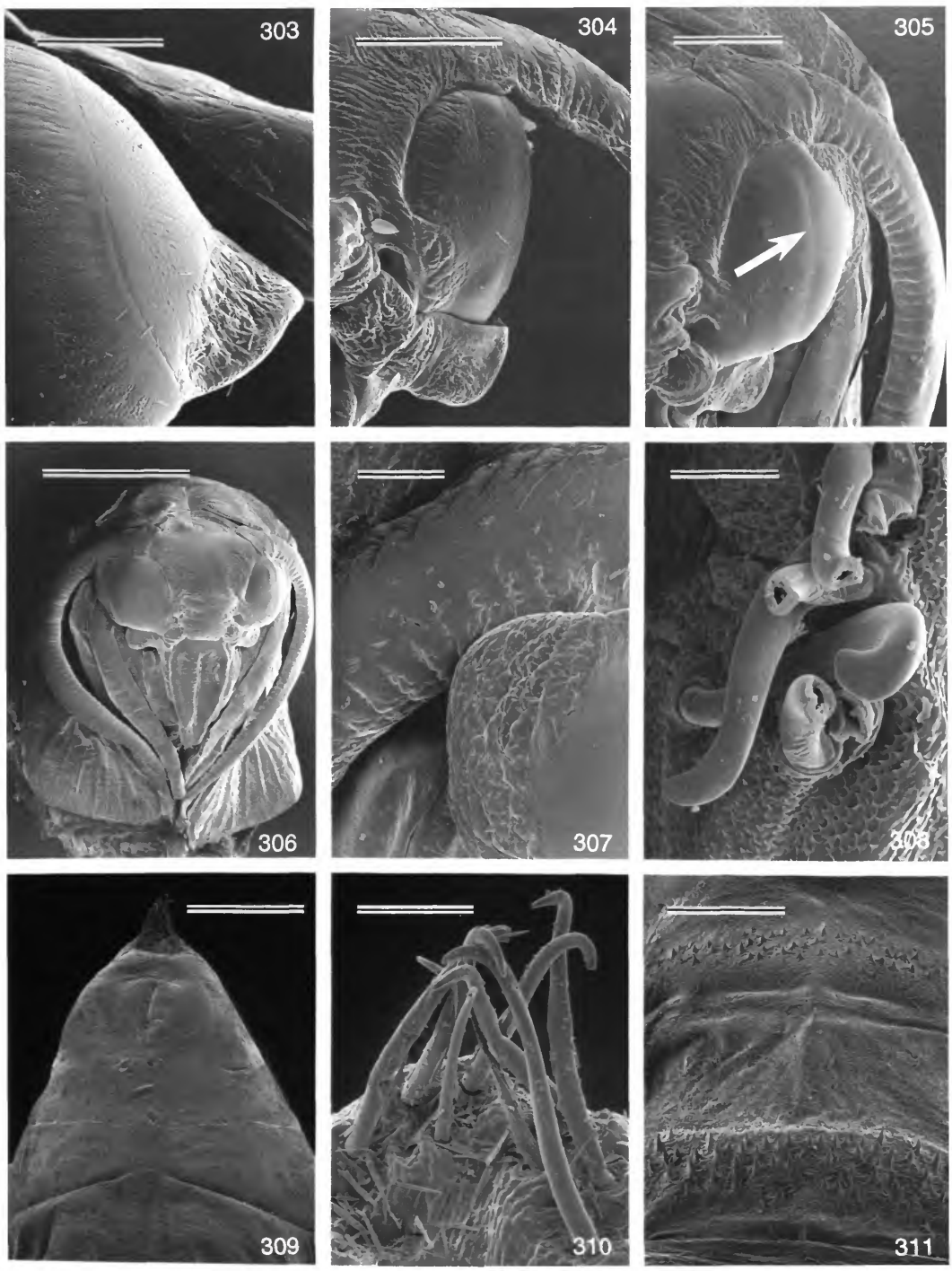
Stiff abdominal setae on the pupal dorsum, directed posteriorly (Figure 311), may prevent pupae in the limacodid group from back-sliding while projecting from the cocoon prior to eclosion. Cremaster hooks may be either present (Figures 308–310) or absent.

Phylogenetic Analysis

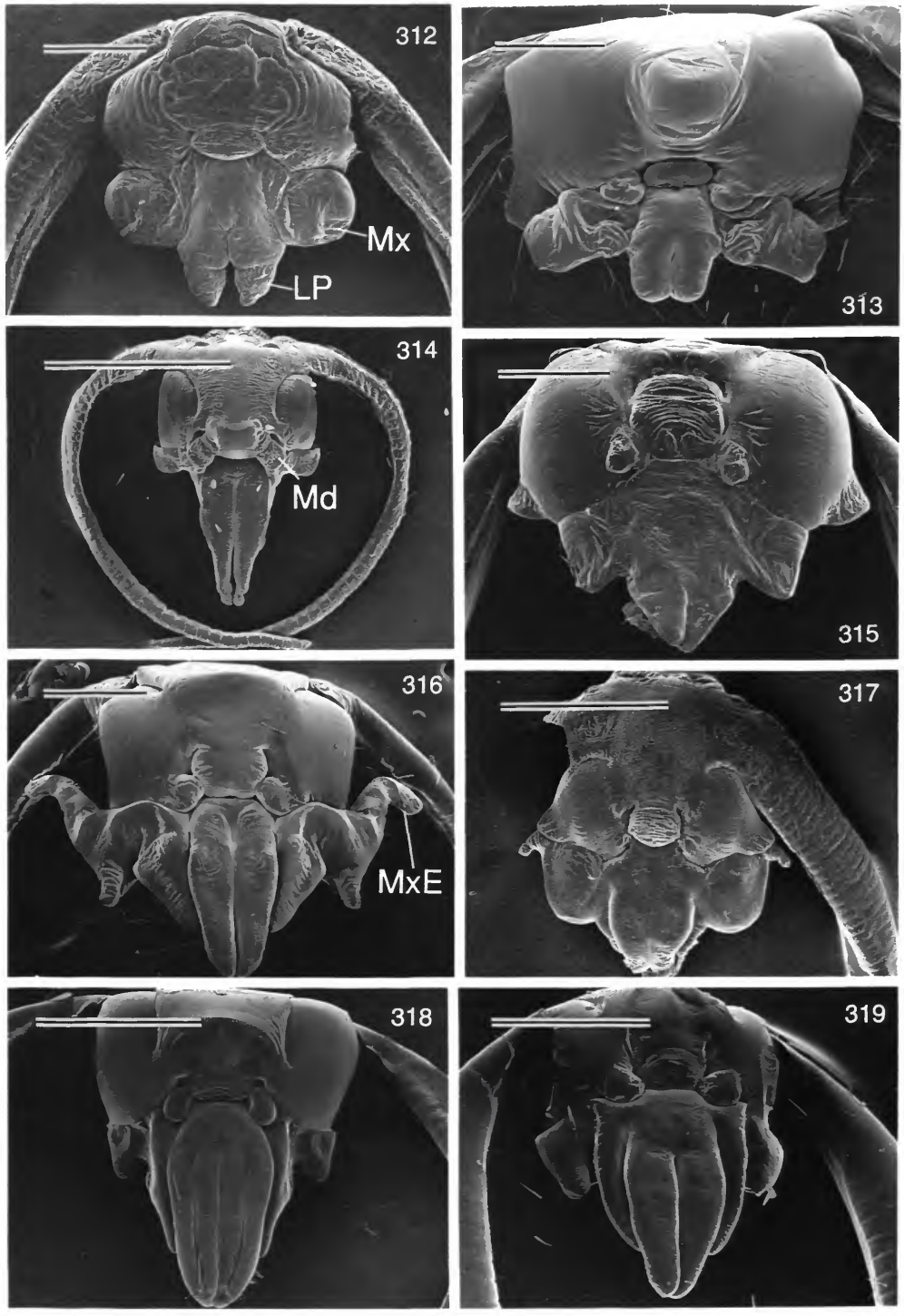
DATA ANALYSIS.—Reliance on characters of either adults (Brock, 1971) or immatures (Common, 1975; Minet, 1986) for the limacodid group and its allies has led to different theories concerning membership of the Cossoidea and Zygaenoidea (see "History of Classification of the Limacodid Group," above). Therefore, independent data sets of adult- and immature-stage characters for phylogenetic analyses were used. Following the initial analyses, the data sets were combined to compare the influences of each. The outgroup method was used to polarize the characters (Maddison et al., 1984).



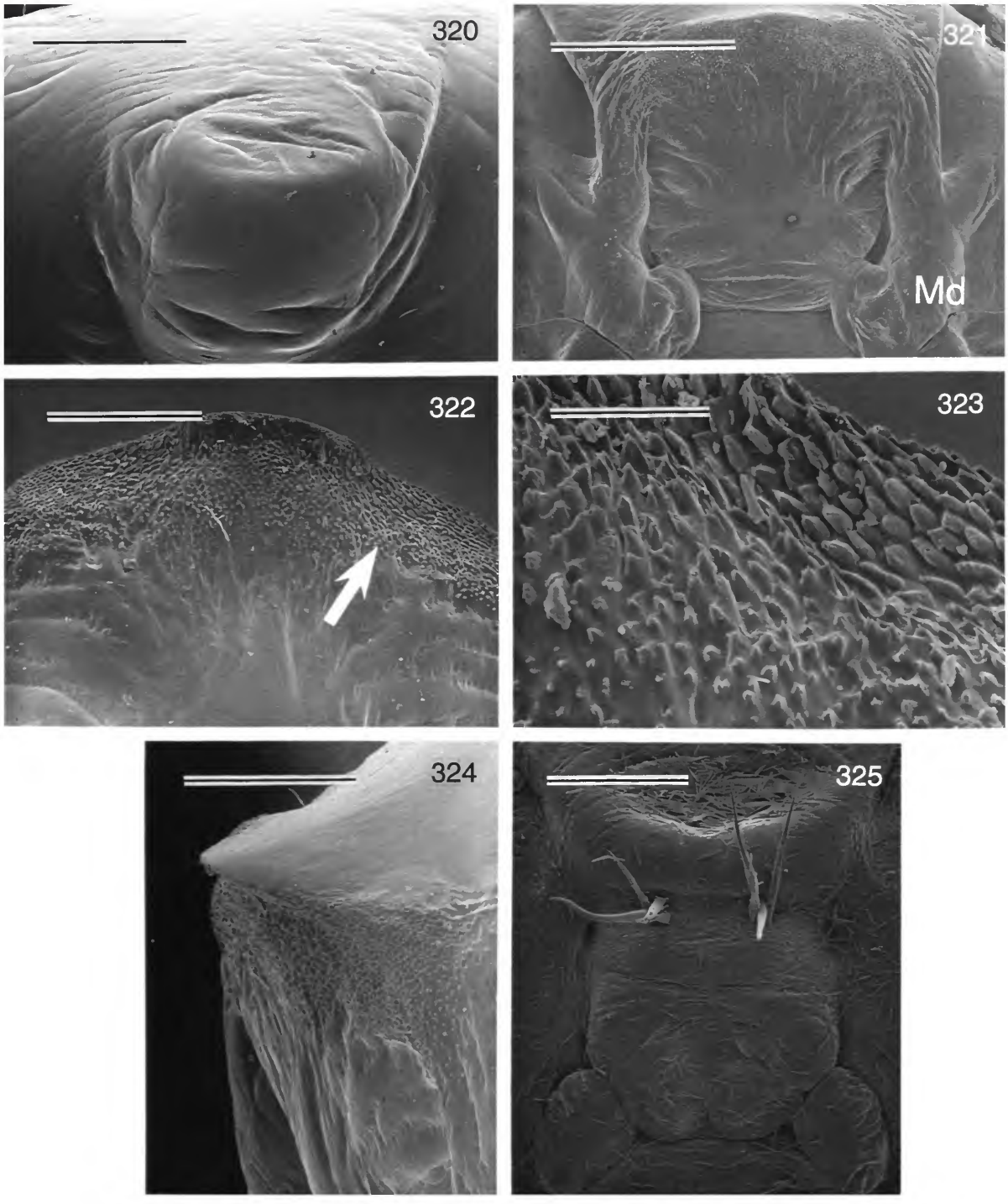
FIGURES 299–302.—Pupa of Megalopygidae (*Megalopyge lanata*) (299–301 photos by L. Minor-Penland): 299, ventral female (length = 27 mm); 300, dorsal male (arrow points to longitudinal depression on mesonotum, similar to adults); 301, ventral male (length = 22 mm); 302, detail of female abdominal spiracles and sensilla, anterior below (sensilla similar to larvae) (scale = 1 mm) (photo by C. Hansen). (SpS = spiracular sensillum, Sp = spiracle.)



FIGURES 303–311.—Detail of pupae in Limacodidae and Dalceridae (scale length in parentheses): 303, sculptured eyepiece in eclosed pupa of *Dalcerides ingenita* (Dalceridae) (200 μm). 304–308, *Semyra coarctata* complex (Limacodidae): 304, eclosed pupa minus eye and sculptured portion (500 μm); 305, uneclosed pupa with sculptured eyepiece (arrow points to fracture line) (500 μm); 306, head and wings of uneclosed pupa (2 mm); 307, detail of antenna and sculptured eye (200 μm); 308, cremaster (50 μm). 309–311, *D. ingenita:* 309, posterior end of abdomen, ventral view (0.6 mm); 310, cremaster, ventral view (86 μm); 311, dorsum of A8 (above) and A9 (0.38 mm).



FIGURES 312–319.—Pupal head (scale length in parentheses): 312, *Aidos yamouna* (Aididae) (1 mm); 313, *Megalopyge* nr. *melaina* (Megalopyginae) (1 mm); 314, *Semyra coarctata* complex (Limacodidae) (2 mm); 315, *Dalcerides ingenita* (Dalceridae) (500 μm); 316, *Acharia* sp. (Limacodidae) (1 mm); 317, *Chrysopoloma similis* (Chrysopolominae) (2 mm); 318, *Euprosterna* sp. (Limacodidae) (1 mm); 319, *Monoleuca semifascia* (Limacodidae) (1 mm). (LP = labial palpus, Md = mandible, Mx = maxilla, MxE = maxillary extension.)



FIGURES 320–325.—Detail of frontal portion of pupal head (scale length in parentheses): 320, *Megalopyge* nr. *melaina* (Megalopyginae) (500 µm). 321–324, *Phobetron pithecium* (Limacodidae): 321, frons and mandibles (500 µm); 322, dorsal ridge of frons, frontal view (200 µm); 323, detail of 322 (see arrow) (50 µm); 324, frontolateral view (200 µm); 325, setae on frons in *Dalcerides ingenita* (Dalceridae) (231 µm). (Md = mandible.)

Hennig86 (Farris, 1988) was used for parsimony analyses of the two independent data sets. The adult- and immature-stage data had 18 (11 multistate) and 25 characters (8 multistate), respectively (Tables 4, 5). Larval characters included early and late instars. The total number of steps of the character state transformations for each cladogram was measured as the length (L). The fit of characters to the cladograms was measured by the consistency index (CI) (Kluge and Farris, 1969) and by the retention index (RI) (Farris, 1989). Multistate character states were ordered into morphoclines from the zygaenid outgroup (Mickevich and Weller, 1990), and the analysis was performed using the ordered default in Hennig86 (the unordered option was also used for comparison) (Farris, 1988).

The Zygaenidae were chosen as the outgroup because they have the largest number of potentially synapomorphic character states with the limacodid-group families. These include the visible first abdominal spiracle of the pupa, uniordinal crochets

TABLE 4.—Taxonomic characters and codes used in phylogenetic analysis (0 = plesiomorphic condition, 1-3 = apomorphic conditions).

CHARACTERS OF ADULTS

Head

1. Labial Palpi: (0) 2 segments, not reaching vertex; (1) 3 segments, porrect, nearly equal length or distal segment 1/3 length of middle segment; (2) 2 segments, porrect, reaching vertex.
2. Chaetosema: (0) present; (1) absent.
3. Galea: (0) very long, much > head width; (1) short, often < head width; (2) absent.
4. Ocellus: (0) present; (1) absent.

Thorax

5. Forewing radial veins, R_{1-3}: (0) independent; (1) R_1 and R_2 branched; (2) R_2 and R_3 branched.
6. Forewing radial veins, R_{3-5}: (0) independent or R_3 and R_4 branched from end of discal cell; (1) R_3 and R_4 branched off vein beyond discal cell; (2) R_4 and R_5 branched.
7. Hindwing discal cell and $Sc + R_1$: (0) $Sc + R_1$ anastomoses with Rs for length of cell (at least midway); (1) $Sc + R_1$ anastomoses with Rs for length of cell in female only (Megalopyginae); (2) $Sc + R_1$ branches from Rs at base, both sexes (in Aididae, R_1 anastomoses with Rs for length of cell, anastomoses with Sc beyond cell).
8. Mesepimeron: (0) broadly sclerotized; (1) narrowly sclerotized.
9. Mesonotum: (0) anterior simple; (1) anteromedial groove.
10. Tibial spurs: (0) 1 pair on mid- and 2 pair on hindleg; (1) 1 pair on mid- and hindleg; (2) absent.
11. Ventral surface of 5th tarsomere: (0) monomorphic; (1) dimorphic, sensilla trichodea only on female and restricted to distal portion; (2) dimorphic, sensilla trichodea only on female and intermixed with scales; (3) dimorphic, without scales, usually as a recessed pad.

Male genitalia

12. Uncus: (0) broad and gently tapering; (1) narrow, sclerotized hook; (2) reduced or absent.
13. Gnathos: (0) absent; (1) present.
14. Juxta: (0) paired processes, sometimes arising from plate; (1) simple.
15. Valvae: (0) wide relative to aedeagus and juxta; (1) digitate and narrow, dorsal; (2) reduced or absent.

Female genitalia

16. Papillae anales (ovipositor lobes): (0) small, lobes flat and open, perpendicular to abdomen, entire; (1) lobes appressed; (2) large, flat and open, moderately or deeply cleft; (3) large, disk shaped, sometimes emarginate.
17. Dense scale pouch on female 7th segment: (0) absent; (1) present.
18. Large secondary accessory glands: (0) present, empty into oviduct; (1) absent; (2) present, external ducts.

CHARACTERS OF IMMATURES

Larva

19. Stemmata: (0) stemma 5 disjunct ventrally, removed > 1.5 × width of 1 stemma from stemma 4; (1) stemma 5 closer to stemma 4, ~ width of 1 stemma from stemma 4.
20. Stemmatal setae on head: (0) S1 and S2 present; (1) only S1 present.
21. Labrum (anterior margin): (0) normal spines; (1) dense spines in medial region; (2) dense spines over entire margin.
22. Spinneret (labium): (0) tubular; (1) narrow opening, laterally expanded, brush-like.
23. Thoracic legs: (0) easily visible, length > width of labrum; (1) small to minute, ≤ width of labrum.
24. Axial seta between hook and base of pretarsal claw: (0) short and rounded; (1) conical or hair-like, sometimes reaching hook.
25. Abdominal segments with prolegs or suckers: (0) A3–A6 and A10 with prolegs; (1) A2–A7 and A10 with prolegs; (2) A2–A7 and A10 with vestigial prolegs (A1–A8, with or without suckers).
26. Abdominal segments A2–A7 with crochets in final instar: (0) crochets on A3–A6 (prolegs present or absent on A2 and A7; segments with prolegs without membranous pad); (1) crochets on A2–A7 (crochets often absent; A2–A7 prolegs with membranous pads or A2–A7 with vestigial prolegs and slug-like ventrum); (2) crochets absent.
27. Abdominal segment A10 with crochets in final instar: (0) present; (1) absent.
28. Presence of crochets in first two instars: (0) present; (1) absent.
29. Length of ventrum of segments A8 and A9 relative to dorsum: (0) normal; (1) narrow, ~ length of 1 segment on dorsum.
30. Texture of ventral surface at base of prolegs A1–A9 and thoracic legs: (0) spinulose; (1) smooth.
31. Distinct membranous pads on prolegs A2–A7: (0) absent; (1) present.
32. Frass flipper on anal prolegs: (0) absent; (1) present.
33. Anal fork: (0) present; (1) absent.
34. Dorsum of A10 (anal plate): (0) normal; (1) reduced, below dorsum of A9.
35. V setae on thorax, V and SV setae on abdomen: (0) hair-like; (1) fungiform.
36. L setae on abdomen: (0) a number of secondary setae (verrucae); (1) 2 primary setae below spiracle; (2) 2 primary setae in line with spiracle.
37. D and SD setae: (0) plumose and spiny setae together; (1) spiny setae or tactile setae after the first instar; (2) primary setae with smooth, gelatinous covering.
38. Digitate spiracle sensilla: (0) absent; (1) on T1, A1–A7.

Pupa

39. Eyepiece: (0) simple; (1) sculptured flange.
40. Labial palpus: (0) width much < width of tibia; (1) ~ equal to width of tibia.
41. Maxilla: (0) long proboscis, reaching length of forewing costa; (1) lobes, much shorter than forewing costa; (2) additional lobe, parallel and ≤ adjoining labial palpus.
42. Cocoon prior to eclosion: (0) ellipsoid, with trap-door end truncate, lid often visible; (1) ovoid, no visible lid; (2) diffuse with inner chamber.

Egg

43. Shape: (0) flat, scale-like, thick chorion; (1) ovoid; (2) flat, scale-like, thin chorion.

TABLE 5.—Character matrix of taxa used in phylogenetic analysis of adults and immatures. Character numbers correspond to the list in Table 4 and Figure 326 (0 = plesiomorphic, 1–3 = apomorphic). Numbers in superscript refer to homoplastic alternate character states found in the taxon.

	Characters of Adults																	
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Zygaenidae	0	0	0	0	0	0	0	0	0^1	0	0	1	0	1^0	0	0	0	0
Megalopyginae	0	0	2	1	0	2	1	0	1	1	2	1	0	0	1	1	1	1
Trosiinae	0	0	1	1	0	2	0	0	1	1	2	1	0^1	0	1	1	1	1
Aididae	1^2	0	2	1	1	1	2	0	1	1	3	0	0	0	0	2	0	0
Dalceridae	2	1	1	1	2	2	2	1	0	2	1	2	1	0	2	2	0	2
Pantoct/Croth	1	1	1	1	0	1	2	1	0	0	1	0	1	1	0	3	0	1
Limacodidae	1	1	1	1	0	1	2	1	0	0	3	0	1	0^1	0	3	0	1

	Characters of Immatures																							
Taxon	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Zygaenidae	0^1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0^1
Megalopyginae	1	0	0	0	0	0	1	1^0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	1	0	1
Trosiinae	1	0	0	0	0	0	1	1^0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	1	0	1
Aididae	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0^1	1	0	1	1	0	1	1	1	0	1
Dalceridae	1	1	1	1	1	1	2	1	1	1	1	1	0	1^0	1	1	1	2	2	0	1	1	1	2	1
Pantoct/Croth	0	1	1^0	1	1	1	2	1	0	1	1	1	0	0	1	1	1	1	1	0	1	1	2	0	1
Limacodidae	0	1	2	1	1	1	2	2	1	1	1	1	0	1^0	1	1	1	1	1^2	0	1	1	2	1	2

in mesoseries (rare in Apoditrysia), arrangement of setae or verrucae, and retractile head of the larva. Although adult synapomorphies are more problematic, the presence of secondary accessory glands in females is a potential synapomorphy. The Cossidae were not used as an outgroup because little evidence was found for synapomorphies between adult or immature stages with the limacodid group; however, character states of cossids and other families in Apoditrysia were useful in determining character codes for adult Zygaenidae.

Ingroup terminal taxa represented families Limacodidae (minus *Pantoctaenia* and *Crothaema*) and Dalceridae and previous megalopygid subfamilies Megalopyginae, Trosiinae, and Aidinae. Both Trosiinae and Megalopyginae, although having nearly redundant characters (excluding autapomorphies), were included to test the position of "Aidinae." "Chrysopolomidae" was not included because preliminary evidence suggested synapomorphies with limacodid lineages (see Chrysopolominae section, below). Epipyropidae, Cyclotornidae, and Heterogynidae, although considered to be within Zygaenoidea (Common, 1990), were not included in the analysis because, at present, no synapomorphies could be found with the limacodid group at a level below Zygaenoidea. Furthermore, they could be members of clades presently within Zygaenidae that were not included in the analysis. Somabrachyidae was not included due to incomplete character data.

Pantoctaenia and *Crothaema* (Limacodidae) were combined and included in a second analysis, with the adult- and immature-stage data sets analyzed separately as well as combined, to test the monophyly of the Limacodidae. These two genera exhibit potentially plesiomorphic character states also found in Dalceridae (e.g., late instar *Pantoctaenia gemmans* has crochets). *Crothaema* was combined with *Pantoctaenia* because these genera share a number of traits not found in other limacodids. Furthermore, pupal and cocoon character states from *Crothaema* were used to supplement missing data for *Pantoctaenia*.

Character data assigned to the limacodid-group taxa are from specimens in Table 1 and from the following: Hopp (1927, 1930) for Megalopygidae; Miller (1994) for Dalceridae; Janse (1964), Holloway (1986), Holloway et al. (1987), and Epstein (1988) for Limacodidae. Adult character states assigned to the zygaenid outgroup were from subfamilies Zygaeninae and Procridinae and were taken from Alberti (1954), Naumann (1977), Tarmann (1984), and specimens in the USNM collection. Larval zygaenid characters were from examination of USNM and Naumann specimens and from descriptions by Dyar and Morton (1895), Forbes (1910, 1923), Fracker (1915), Tremewan (1985), and Stehr (1987c). Pupal zygaenid characters were from examination of USNM specimens and from Mosher (1916), whereas egg characters were from USNM specimens and from Peterson (1967), Common (1990), and Fehrenbach (1995).

RESULTS AND DISCUSSION.—The first set of analyses using independent character data from immature and adult stages resulted in the same most-parsimonious cladogram (Figure 326, minus *Pantoctaenia/Crothaema*). The megalopygid subfamilies Trosiinae and Megalopyginae were monophyletic and arose from the base of the limacodid group. Aididae formed a monophyletic group with Limacodidae + Dalceridae. Synapomorphies supporting this hypothesis are listed in Table 6 and are shown in Figure 326. Tree length (L), consistency index (CI), and retention index (RI), from each analysis, are summarized in Table 7.

Although the results of the first set of analyses produced

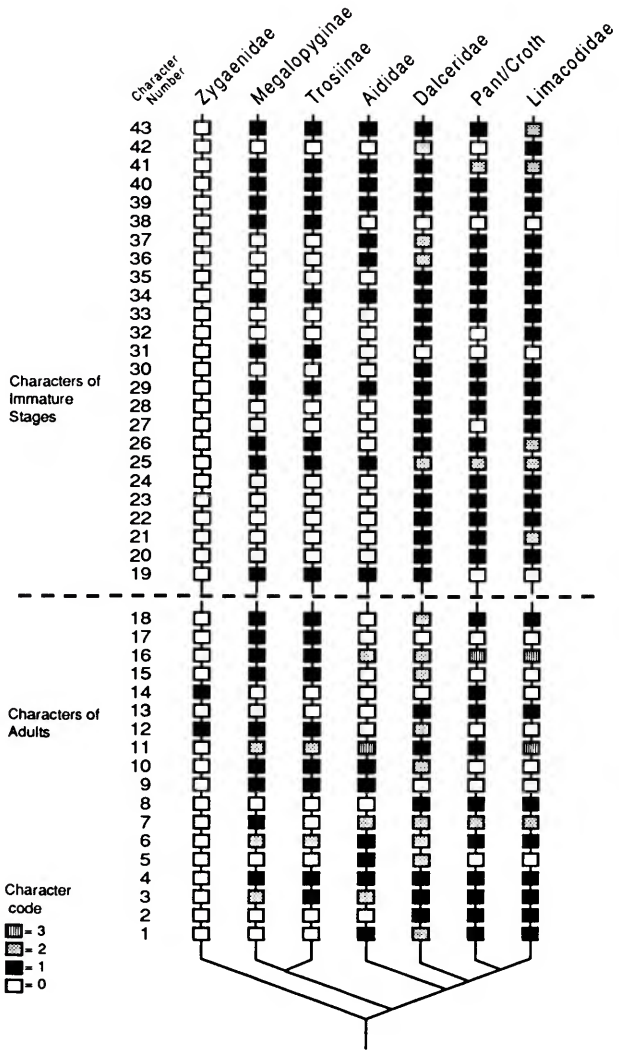


FIGURE 326.—Cladogram of limacodid group based on parsimony analysis of adult and immature-stage characters, with Zygaenidae as outgroup. Shaded rectangles represent character codes for synapomorphies; multiple-state characters with lower numbers are plesiomorphic compared to those with higher numbers. Character numbers and states correspond to descriptions in Table 4 and matrix in Table 5. Numbers 1–18 and 19–43 refer to adult and immature-stage data, respectively. Taxon "Pant/Croth" represents a combination of characters found in *Pantoctaenia* and *Crothaema* (Limacodidae).

cladograms congruent between immature and adult stages, the inclusion of *Pantoctaenia/Crothaema* produced two cladograms. The adult and combined charater data placed Dalceridae as the sister group to Limacodidae + *Pantoctaenia/Crothaema*, whereas characters of the immatures showed *Pantoctaenia/Crothaema* to be the sister group of Dalceridae + Limacodidae.

The different cladogram based on the character data of immature stages is explainable by two "synapomorphies" for Limacodidae + Dalceridae, each related to the anal proleg: (1) the presence of frass-flipping setae below the anus (character 32), and (2) the absence of crochets in mature larvae (character 27). These synapomorphies may be flawed, as indicated by the results of the adult and combined data sets. In *Pantoctaenia* the absence of frass-flipping setae may result from a secondary loss rather than from plesiomorphy (as treated here). This is suggested by the absence of these setae in a number of limacodids (Figure 296) and in some dalcerids (Figure 276). Furthermore, crochets on A10 may have been lost independently in both limacodids and dalcerids rather than the absence being a synapomorphy, because throughout the limacodid group similar losses appear to have occurred on A2 and A7. In order to test the influence of the two characters, I recoded character 32 in *Pantoctaenia/Crothaema* as a loss, rather than as a plesiomorphy, and I recoded character 27 as a convergent loss in limacodids and dalcerids. I used linear coding for character 27 to allow transformation of each loss of A10 crochets from the plesiomorphic condition (Mickevich and Weller, 1990). This resulted in congruence with the adult data set (L = 38, CI = 0.92, RI = 0.90).

Transitional character states (morphoclines) between zygaenids and limacodids, as noted by Dyar (1894) and Fracker (1915), are more fully understood with new or recently discovered character data for megalopygids, aidids, dalcerids, and limacodids. These morphoclines and the complexity of larval synapomorphies provide strong support for unifying these families with external-feeding larvae into one superfamily (e.g., Zygaenoidea sensu Common) rather than separating them into different superfamilies, as proposed by Brock (1971) and Heppner (1984) (see "History of Classification of the Limacodid Group," above).

Many transitional larval characters on the cladogram (Figure 326) involve reductions, except for the addition of two pairs of abdominal prolegs with crochets in the limacodid-group hypothetical ancestor (characters 25, 26). Graphical representation of the proleg transformation series (Figure 327) illustrates reduction in relative proleg length from the ancestral zygaenid condition. In the limacodid-group ancestor, these transitions involve the shortening and widening of prolegs, reduction of the anal plate (character 34), and compression of the ventral portion of segments A8 and A9 (character 29). A change in the L and SV rows from multiple secondary setae to primary setae in the aidid + (limacodid + dalcerid) clade can be interpreted as a reduction (Figure 327) or as a change in the developmental clock in which primary setae do not transform or progress into verrucae (with multiple secondary setae) (see further discussion under "Homology and Evolution of Larval Body Setae," below). Reductions in the limacodid + dalcerid hypothetical ancestor include (1) thoracic leg size (character 23); (2) size of the V1 seta at the base of thoracic legs and of V and SV setae on the abdomen (character 35); and (3) proleg size and crochet size and number. Shagreened cuticle has apparently been lost

TABLE 6.—Apomorphic characters in the limacodid group.

Taxon	Immature	Adult
	Synapomorphies	
LIMACODIDAE + DALCERIDAE	1. fungiform setae (SV and V) on ventral surface	1. chaetosemata absent
	2. crochets absent in 1st 2–3 instars	2. reduced sclerite on mesepimeron
	3. prolegs highly reduced on A2–A7	3. gnathos present
	4. brush-like spinneret	
	5. reduced thoracic legs	
	6. stemmata with S1 seta only	
	7. anal fork absent	
	8. elongate axial setae	
	9. frass-flipping setae	
	10. ventral surface smooth	
AIDIDAE + (LIMACODIDAE + DALCERIDAE)	1. plumose setae absent	1. papillae anales open and flat, cleft
	2. primary L setae on abdomen	2. labial palpus porrect, reaching vertex or beyond
		3. hindwing Sc + R_1 branches from base of discal cell (both sexes)
MEGALOPYGIDAE + (AIDIDAE + (LIMACODIDAE + DALCERIDAE))	1. abdominal prolegs on A2–A7, with crochets	1. ocelli absent
	2. length of A8–A9 reduced beneath	2. short galeae
	3. anal plate reduced, without verrucae	3. female 5th tarsomere with dense sensilla trichodea beneath
	4. prolegs short	4. branched forewing R_3 and R_4 or R_4 and R_5 stalked beyond discal cell
	5. pupal maxilla shorter than labial palpus	
	6. sculpted flange on pupal eyepiece	
	Autapomorphies	
LIMACODIDAE*	1. crochets absent, all instars	1. female legs with recessed pad of sensilla trichodea underneath
	2. flat, thin eggs	2. disk-shaped papillae anales, entire
	3. extended pupal maxilla, contiguous with labial palpus	
	4. hard, ovoid cocoons, lid invisible when uneclosed	
DALCERIDAE	1. gelatin-covered setae, all instars	1. uncus highly reduced
	2. cocoon without lid, with ovoid inner chamber	2. valvae reduced or fused
	3. L setae on abdomen above or in line with spiracles	3. female accessory glands with external ducts
		4. forewing R_2 and R_3 stalked
AIDIDAE	1. spinneret with amorphous tip	1. forewing R_1 and R_2 stalked
	2. cocoons with 1 or 2 pairs of holes in outer mesh	2. male antennae bipectinate in basal two-thirds
MEGALOPYGIDAE	1. digitate sensilla proximal to all spiracles	1. dense pack of pilose scales on end of female abdomen
	2. prolegs A2–A7 with large, membranous pads	2. valvae reduced to small digitate lobes
		3. forewing R_2–R_4 pectinate off R_5

* Characters in Limacodidae (+ Chrysopolomidae) do not include those of *Pantoctaenia* and *Crothaema* (except autapomorphy 3 of immature and autapomorphy 2 of adult).

TABLE 7.—Tree length (L), consistency index (CI), and retention index (RI) for phylogenetic analyses. The second group of analyses included the additional terminal taxon *Pantoctaenia/Crothaema*.

Life stage	First group of analyses			Second group of analyses		
	L	CI	RI	L	CI	RI
Adults	42	0.73	0.54	44	0.70	0.59
Immatures	34	0.91	0.85	37	0.86	0.85
Combined data	76	0.81	0.68	82	0.76	0.71
Unordered	70	0.88	0.75	75	0.84	0.79

on ventral A1–A9 in the limacodid + dalcerid ancestor (character 30). Reductions within Limacodidae (excluding *Pantoctaenia*) include the complete loss of crochets and the reduction in size of thoracic leg setae.

Genitalia do not follow smooth transitions as in characters of the immature stages, perhaps due to homology problems. The gnathos in the limacodid + dalcerid clade (character 13) is of questionable homology with the structure found in the Tineoidea and the lower Ditrysia because it has been lost in the Zygaenidae (Kuznetsov and Stekol'nikov, 1981; Common, 1990), Megalopygidae, and Aididae. A gnathos-like structure may have been derived, perhaps from transtillar lobes like those found in the Chrysopolominae, as suggested in zygaenids by Kuznetsov and Stekol'nikov (1981). Although not coded as having the same character condition, independent reductions of the male valvae in megalopygids and dalcerids may be related to specialized aspects of the female ovipositor (character 15). The dense clump of piliform scales on female megalopygids (character 17) and the external ducts for sticky secretions in dalcerids (character 18) could make lateral clasping by typical valvae more difficult. The absence of large accessory glands in female limacodids and megalopygids (character 18) may be considered convergent, secondary losses. This is supported by the presence of these glands in other members of the limacodid group and in the Zygaenoidea; the glands occur in dalcerids, aidids, zygaenids, cyclotornids, and epipyropids.

There is less homoplasy in the two analyses of immature-stage characters (CI = 0.91 and 0.89) compared to the two analyses of adult characters (CI = 0.73 and 0.70). Examples of homoplasy in the larval characters include the absence of crochets on segments A2 and A7 in aidids (character 26). This is likely to be a secondary loss rather than the plesiomorphic condition found in zygaenids (see further discussion under "Prolegs and Crochets," below). The close proximity of stemma 5 to stemma 4 in limacodids (+ *Pantoctaenia*) may be a reversal to the zygaenid condition (character 19); however, some confusion exists due to variation of this character state within zygaenids (see "Morphology," above).

Examples of homoplasy in the adult characters, in addition to those given above, include the number of spurs on the hindtibia (character 10). The configuration 0-2-4 occurs in zygaenids and does not appear in my cladogram until limacodids, indicating a gain from the 0-2-2 condition in megalopygids and aidids. The absence of tibial spurs in the Dalceridae is hypothesized to have been from a common ancestor with limacodids that had 0-2-2 or 0-2-4. Limacodid genera with the largest number of

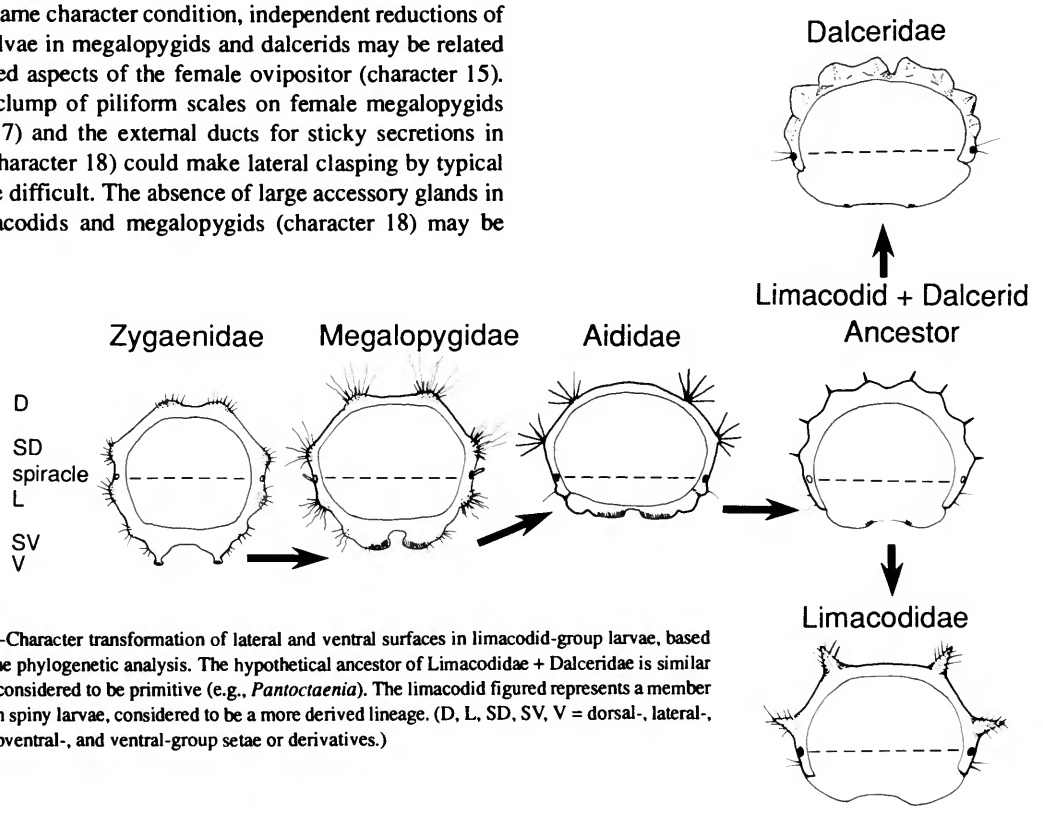


FIGURE 327.—Character transformation of lateral and ventral surfaces in limacodid-group larvae, based on results of the phylogenetic analysis. The hypothetical ancestor of Limacodidae + Dalceridae is similar to limacodids considered to be primitive (e.g., *Pantoctaenia*). The limacodid figured represents a member of a group with spiny larvae, considered to be a more derived lineage. (D, L, SD, SV, V = dorsal-, lateral-, subdorsal-, subventral-, and ventral-group setae or derivatives.)

plesiomorphies in the larval stage (e.g., *Pantoctaenia*) all have the 0-2-4 condition. The branching of forewing R_4 and R_5 (character 6) in dalcerids appears to be convergent with the condition found in megalopygids.

Alexander (1990), for nomadine bees, and Miller (1991), for notodontid moths, also found more homoplasy in cladograms generated using characters of adults compared to those generated from characters of immature stages. Underlying causes were believed to include problems of homology in adult genitalia (Miller, 1991) and slower evolution and the conservation of novel features in larval forms (Alexander, 1990). The occurrence of larval transitional forms in my cladogram may be a byproduct of slow evolution, as referred to by Alexander (1990). In contrast to Miller (1991), I found the homoplasy in adults to be equally distributed in the three body regions. In several examples, I suspect that homoplasy resulted from loss of characters that were found in ancestral taxa. This is based on the presence of these ancestral states in both lower and higher lineages on the cladogram (Figure 326). Examples include the absence of secondary accessory glands in megalopygids and limacodids (character 18) and the absence of galeae in megalopygines and aidids (character 3). Similar examples in the larval stage include characters 27 and 32, discussed above, and the absence of crochets on A2 and A7 in aidids and in a number of megalopygids and dalcerids (character 26) (see "Evolution of the Ventral Abdominal Surface," below).

Keys to Limacodid-Group Families and Allies

The following keys to adults and larvae primarily discriminate between members of the limacodid group and their allies, which together consitute the Zygaenoidea (sensu Common, 1970). Adults in the limacodid group can be separated from similar Cossidae, Psychidae, and other lower Ditrysia by the absence of the stem of medial veins within the discal cell of the hindwing. They can be separated from the Lasiocampidae, Lymantriidae, and other higher Ditrysia by the presence of a strong CuP in the forewing and the presence of veinlets in the forewing discal cell. Larval Lycaenidae and Riodinidae can be easily confused with Zygaenoidea; lycaenids often have retractile heads, and both groups have a variety of dorsal setae and have short prolegs on A3–A6 and A10, giving them a slug-like appearance. They can often be separated from Zygaenoidea by the mesoseries being divided by a membranous pad. Larval *Olona* (Limacodidae) are included in the key based solely on figures and descriptions in the literature (e.g., Holloway et al., 1987) because I have been unable to examine them.

Key to Adults

1. Ocelli present; commonly diurnal 2
   Ocelli absent; commonly nocturnal 4
2. Forewing R with veins stalked from end of discal cell; females winged . . . . . **ZYGAENIDAE** (in part)
   Forewing R unstalked from discal cell; females winged or apterous 3
3. Wings smokey colored, sparsely scaled and nearly equal in size (males), or wings absent (females); proboscis reduced or absent; Europe and Africa . . . . . **HETEROGYNIDAE**
   Wings often brightly colored, wings present in both sexes; proboscis usually long; Cosmopolitan . . . . . **ZYGAENIDAE** (in part)
4. Forewing R unstalked or only R_4 and R_5 stalked 5
   Forewing R stalked in various combinations or [rarely] wings absent; if R_4 and R_5 stalked without R_3 from discal cell, R_2 and R_3 stalked or fused [Figures 72, 74] 6
5. Forewing triangulate, larger than hindwing; tibial spurs absent; small and dark with bipectinate antennae [Figure 42]; mostly pantropical . . . . . **EPIPYROPIDAE**
   Wings rounded, nearly equal in size; tibial spurs 0-2-4; small with filiform antennae; Australia . . . . . **CYCLOTORNIDAE**
6. Head with sculptured process or less developed wrinkles on frons; chaetosemata present; epiphysis present or absent; Africa or Mediterranean [Figure 47] [wings absent in female *Sombrachys*] . . . . . **SOMABRACHYIDAE**
   Head without process or wrinkles on frons; chaetosemata present or absent; epiphysis absent 7
7. Forewing R_4 and R_5 stalked (if fused, R_2 and R_3 fused) 8
   Forewing R_3 and R_4 stalked (if independent, branch off R_2) 9

8. Forewing R_2 and R_3 independent [Figures 68, 70]; hindwing $Sc + R_1$ fused with Rs along discal cell (all females, males in part) [Figure 68]; labial palpi short and hidden by surrounding scales [Figures 53*a*,*b*]; chaetosemata present; tibial spurs present (0-2-2); females with dense pack of woolly scales on end of abdomen . . . . . **MEGALOPYGIDAE**

   Forewing R_2 and R_3 stalked or fused [Figures 72, 74]; hindwing $Sc + R_1$ independent of Rs along discal cell except at base [Figure 75]; labial palpi curved upward and easily visible [Figures 55, 57*a*]; chaetosemata absent; tibial spurs absent; females with normal scales on end of abdomen . . . . . **DALCERIDAE**

9. Forewing R_1 and R_2 stalked [Figure 69]; chaetosemata present; Neotropics . . . . . **AIDIDAE**

   Forewing R_1 and R_2 independent; chaetosemata absent 10

10. Frenulum and gnathos absent; hindwing large, nearly equal in size to forewing [Figure 50]; forewing R_3 and R_4 stalked or independent, branch off R_2; male antenna bipectinate to apex; Africa and Madagascar . . . . **CHRYSOPOLOMINAE**

    Frenulum and gnathos present; hindwing usually smaller than forewing [Figures 51, 52]; forewing R_3 and R_4 stalked (unless fused), branch off R_5, R_2, or in-between [Figures 71, 73]; male antenna bipectinate to apex, filiform, or many conditions in between; Cosmopolitan . . . . . **LIMACODIDAE**

Key to Larvae

1. Dorsum with spiny and/or hairy verrucae, scoli, or tubercles or with smooth, nondeciduous warts 2

   Dorsum without verrucae, rarely with primary setae covered with gelatinous warts that are deciduous and translucent 8

2. Prolegs on segments A3–A6 and A10 3

   Prolegs on segments A2–A7 and A10, or ventral surface slug-like 5

3. Dorsum with smooth warts. **ZYGAENIDAE** (in part) . . . . . ***Lactura,*** see Common, 1990

   Dorsum with hairy or spiny verrucae 4

4. Verrucae with spiny setae . . . . . **ZYGAENIDAE** (in part)

   Verrucae without spiny setae; Africa and Mediterranean . . . . **HETEROGYNIDAE**

5. Dorsum of T2, T3, and A1–A9 with spinose verrucae or scoli, or hairy tubercles; L row with 2 primary, often hair-like setae; slug-like ventral surface frequently with visible suckers (A1–A8) [Figure 222] . . . . . **LIMACODIDAE** (in part)

   Dorsum of T2, T3, and A1–A9 with spinose verrucae; L row with verrucae or smooth warts; prolegs distinct on A2–A7 and A10 [Figures 215–218, 223] . . 6

6. Each spiracle with 1 digitate sensillum [Figures 328–334]; anterior portion of prolegs with membranous pads and 2 stout SV setae [Figures 256, 257]; D and SD verrucae often bearing both plumose and spinose setae [Figures 166, 169]; L and SV rows with verrucae; New World . . . . . **MEGALOPYGIDAE**

   Each spiracle without digitate sensillum; prolegs without membranous pads; D and SD verrucae bearing primarily spinose setae [Figures 167, 336, 337]; L and SV rows with or without numerous setae 7

7. Scale-like setae dorsal to spiracles or oval pouch filled with minute hairs; L and SV verrucae with hair-like and spinose setae (late instars); D and SD verrucae with spinose [Figure 167] or plumose setae; anal comb present [Figure 280]; Africa and southern Mediterranean . . . . . **SOMABRACHYIDAE**

   No scale-like setae or oval pouch dorsal to spiracles; L and SV rows without verrucae, L row with single primary setae on 2 horizontal warts below spiracle [Figure 339]; D and SD verrucae with spinose setae [Figures 336, 337]; small anal fork present or absent; Neotropics . . . . . **AIDIDAE**

8. Prolegs or crochets present on segments A3–A6 and A10; crochets forming a penellipse or mesoseries; dorsum sometimes with waxy excretions; gelatinous warts absent 9
   Prolegs reduced, ventral surface slug-like, with or without suckers or crochets; dorsum without waxy excretions; gelatinous warts present or absent 10
9. Crochets in a penellipse; Cosmopolitan . . . . . EPIPYROPIDAE
   Crochets in a mesoseries; Australia . . . . . CYCLOTORNIDAE
10. Dorsum smooth or with spinules 11
    Dorsum with gelatinous tubercles 12
11. Long black primary setae with white apex on dorsum; dorsum spinulate [Figure 5]; Africa and Madagascar . . . . . CHRYSOPOLOMINAE
    Short primary setae on dorsum; dorsum smooth or spinulate [Figure 7]; Cosmopolitan . . . . . LIMACODIDAE (in part)
12. Pigmented pattern on dorsum beneath gelatinous warts; Neotropics and southwestern United States . . . . . DALCERIDAE
    Without pigmented pattern on dorsum beneath gelatinous warts; Southeast Asia . . . . . *Olona* (Limacodidae)

Limacodid-Group Families and Allies

This section presents adult diagnoses for each limacodid-group family. Redescriptions for poorly known adults and for immature stages are included. Also presented under each family are discussions of relationships and taxonomic position, as well as reinterpretation of character polarity and homology based on evidence to date. Family status for Aididae reflects the results of my phylogenetic analysis, and Chrysopolomidae is placed as a subfamily of Limacodidae based on morphological evidence presented herein. Often included as a subfamily of Megalopygidae, Somabrachyidae is put at the family level for reasons stated below. Discussion of Epipyropidae and Cyclotornidae does not imply membership in the limacodid group.

MEGALOPYGIDAE Herrich-Schäffer, 1855
(MEGALOPYGINAE and TROSIINAE)

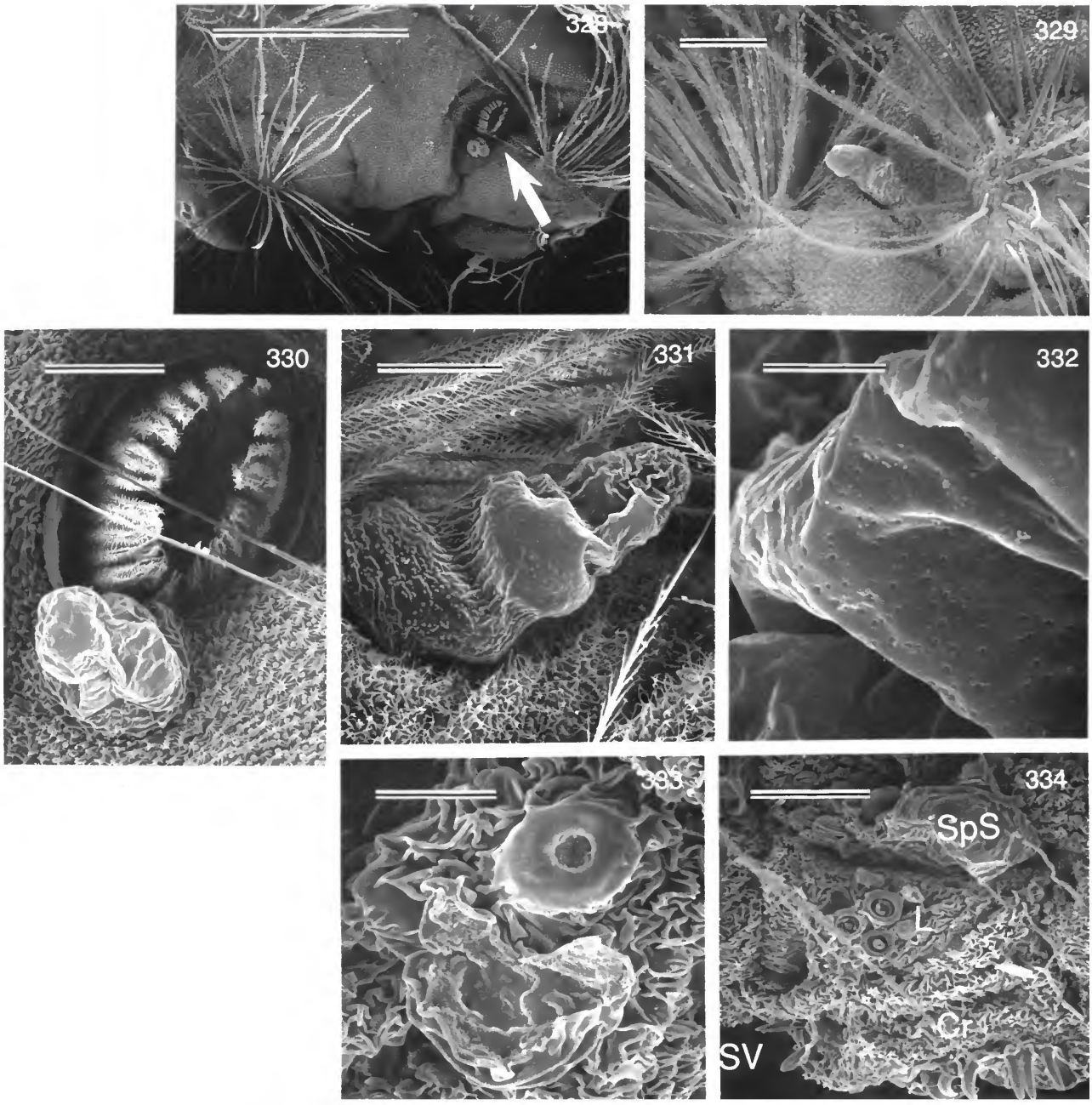
ADULT DIAGNOSIS (Figures 43–46).—Megalopygidae distinguished from other New World limacodid-group families by forewing R_{1-5} forming pectinate branch from radial sector (Figures 68, 70); hindwing $Sc + R_1$ anastomosed with Rs for entire length of discal cell (except male Megalopyginae) (Figure 68); wing scales piliform or cleft, often tripartite; labial palpi short, one- or two-segmented, often hidden by surrounding scales (Figure 53*a,b*); female abdomen with dense tuft of piliform scales on A7 (Figure 46); and female genitalia with papillae anales laterally flattened and medially appressed (Figures 345, 346). Separated from Aididae by male antennae bipectinate to apex (Figures 43–45) and by fifth tarsomere of female with sensilla trichodea beneath intermixed with scales (Figures 76–81); female antennae bipectinate as in males or serrate. Male genitalia differing from Aididae and Limacodidae by short, narrow uncus and small digitate valvae dorsal to juxtal lobes (Figure 351). Mesonotum with longitudinal depressions (Figure 60) and mesepimeron broadly sclerotized (Figure 67). Anterior and posterior apophyses of female well developed (Figures 345, 346).

LARVA (Figures 1, 2, 328–334).—*Head:* Stemma 5 ventrally disjunct by greater than 1 stemma width from others, stemma 4 closer to stemma 6 than to stemma 5 (Figure 119); S1 and S2 setae present (Figure 119); labrum without small epipharyngeal spines on anterior margin (Figures 131–133); spinneret tubular and symmetrical, with dorsal opening near apex (Figures 145–147).

Dorsum: Prothoracic shield with D and SD verrucae combined and with 1 L and 2 distinct SV verrucae below (Figure 166); T2, T3, and A1–A9 with D, SD, and L verrucae of long plumose setae and short, frequently hidden, urticating setae (Figure 169) and with L3 and SV verrucae with plumose setae; T2 with D1 and D2 verrucae contiguous and partially distinct, whereas other D verrucae completely fused; digitate sensilla proximate to each spiracle (Figures 328–334).

Ventrum: Thoracic leg with short, axial seta beneath claw (Figures 228, 229); abdominal prolegs with membranous pad present on segments A2–A7 (Figures 216, 218) and 2 broad setae anterior to and near pad (Figures 252–257). A2 and A7 with or without crochets; crochets on A2–A7 uniordinal in V-shaped mesoseries, divided into anterior and posterior portions or entire (Figure 256); anal proleg (A10) with undivided mesoseries (Figures 278, 284); anal fork with emarginate tip dorsal to anus, below D and SD setae on A10 (Figure 278).

PUPA (Figures 299–302, 313, 320).—Labium of nearly equal width throughout, not tapered toward tip, projecting only



FIGURES 328–334.—Spiracular sensilla in Megalopygidae (scale length in parentheses). 328–330, *Megalopyge crispata:* 328, T1 and T2 (anterior to left), arrow points to T1 spiracle and sensillum (1 mm); 329, T1 spiracular sensillum and L verrucae (anterior to right) (200 μm); 330, T1 spiracle and sensillum, detail of 328 (see arrow) (100 μm). 331, 332, *Mesocia pusilla:* 331, A1 sensillum (anterior to right) (60 μm); 332, detail of sensillum (3 μm). 333, 334, *Megalopyge* sp., 1st instar (BMNH): 333, prothoracic spiracle and sensillum below (23.1 μm); 334, spiracular sensillum, L verrucae, SV setae, and proleg on 3rd abominal segment (50 μm). (Cr = crochets, L, SV = lateral-, subventral-group setae, SpS = spiracular sensillum.)

short distance below lateral portion of maxilla (compare with Limacodidae, Dalceridae, and Aididae). Mesonotum with longitudinal depression as in adults (Figure 300). Spiracles on A1–A6 with lobes similar to digitate sensilla of larva in females (Figure 302); lobes only distinct on A1 in males. Unopened cocoons (Figure 14) often with visible escape hatch (compare with Limacodidae).

DISCUSSION.—Character states of adult Megalopygidae are given by Hopp (1927, 1934). He divided Megalopygidae into three subfamilies (Megalopyginae, Trosiinae, and Aidinae) and suggested that trosiines were the most generalized megalopygids based on hindwing venation and male genitalia (Hopp, 1934).

Although there is strong evidence to support a monophyletic Megalopyginae + Trosiinae (Figure 326, Table 6), Hopp's generic assignments for these subfamilies require future work. A sister-group relationship between "Aidinae" and Trosiinae or Megalopyginae is not supported by synapomorphies. Furthermore, to be monophyletic with either megalopygid subfamily the synapomorphies between Aididae and Limacodidae + Dalceridae (Figure 326, Table 6) would have to have been independently derived in "Aidinae." If new information or a new interpretation of character coding were to support placing Aididae back in the Megalopygidae, perhaps a more plausible hypothesis would be Aidinae as the sister group to Trosiinae + Megalopyginae.

Interpreting the homology of male genitalia in the Megalopygidae (Figure 351) is facilitated by character states of male genitalia in the Aididae (Figures 352, 353). Eyer (1924) and Hopp (1927, 1930) divided the "valva" found in megalopygines and trosiines into a dorsal harpe (= cucullus in Eyer) and ventral sacculus. Neither of them described the male genitalia in aidids, although Hopp (1934:1073) discusses the greater structural modification in trosiines compared to aidines or megalopygines. Birket-Smith (1974) referred to a lobe mesal of the valva and lateral to the juxta in the Cossidae as the valvella. This structure may be homologous with the juxtal lobes, or processes, found in aidids (Figures 352, 353) and dalcerids (Figures 354, 355). Applying this concept to the Megalopygidae, the dorsal lobe is simply the valva, and the lower lobe is the juxtal lobe (Figure 351). The condition found in megalopygids could have been derived from the one in aidids by reduction of the broad valva to a digitate structure, with the juxta remaining as the ventral lobe (further discussed in Dalceridae section, below).

In my phylogenetic analysis, I treat the fusion of hindwing Sc with Rs along the discal cell as plesiomorphic in the Megalopygidae, based on the condition in the Zygaenidae. This was, in fact, the interpretation used by Hopp (1934); according to him, the character went from complete anastomosis (Trosiinae) (Figure 68) to having only the basal portion fused (Megalopyginae) (Figure 70) to having the vein free for the entire discal cell ("Aidinae") (Figure 69). Because the free condition is plesiomorphic for Lepidoptera, however, the polarity of this character is uncertain. It is possible that the fused condition in megalopygids evolved independently of zygaenids, and the condition in Aididae is plesiomorphic.

Traditionally, trosiine larvae (Figure 2) are regarded as being less pilose than their megalopygine relatives (Figure 1). Neither *Mesocia* (Trosiinae) nor *Megalopyge lanata* (Megalopyginae), however, fits this characterization; the former is densely pilose, whereas the latter exhibits verrucae in distinct clumps without pilose setae. One new character of the adults may have utility in separating the two subfamilies. The ventral surface of the fifth tarsomere in female trosiines (Figures 76, 77) appears to have fewer scales versus sensilla trichodea than in female megalopygines (Figure 79).

Fracker (1915:97) described stemma 5 as being close to stemma 4 in megalopygine species *Megalopyge* (= *Lagoa*) *crispata* but distant from stemma 4 in *M. opercularis* (J.E. Smith); however, stemma 5 appears to be distant for *M. crispata* as well (Figure 119). Furthermore, Fracker only mentioned trosiine species *Norape* (= *Carama*) *cretata* (Grote) as having equal distance between stemmata 4 and 1 and between stemmata 4 and 5; this condition also occurs in *M. crispata*.

Homology and function of the spiracular sensilla (Figures 328–334) in megalopygids are not well understood. Packard (1894) indicated that homology with primary setae was unlikely; however, the close proximity of SD2 and L setae to the spiracles in dalcerids and in some limacodids on A1–A8 suggests otherwise. According to Packard's (1894:289) Neo-Lamarckian view, the sensilla evolved from everted glands or osmeteria, which through disuse lost both the ability to retract and secrete "malodorous fluid." He also thought they might be "pleuropodia, or homologues of the temporary embryonic abdominal legs of lower insects."

The spiracular sensilla appear to have a defensive function. When disturbed in the vicinity of the sensilla, the larva will move both SD and L rows of the urticating verrucae towards the sensilla/spiracles in what appears to be a defensive posture; to my knowledge, this was first reported in a megalopygid, misidentified as *Aidos amanda*, by Hoffmann (1932). Similar structures occur in close association with spiracles of pupae (e.g., *Megalopyge lanata*) (Figure 302) (Mosher, 1916), as well as in some adult females.

Crochets equivalent in size and number to those on A3–A6 may occur on prolegs A2 and A7, contrary to previous descriptions of megalopygid larvae (Packard, 1894; Dyar, 1899b; Hopp, 1934). Unfortunately, I have been able to associate only one species possessing these "extra" crochet segments, *Mesocia pusilla* (Trosiinae) from Colombia, with adult vouchers. I examined other undetermined larvae sharing this configuration, including another very distinct trosiine from Veracruz, Mexico (USNM), two presumably megalopygine larvae from Argentina (BMNH), and other specimens from Colombia and Ecuador (USNM).

The size of the membranous pads varies within individuals.

They can be either uniform between prolegs or much larger on A2 and A7, especially in species that lack crochets on these two segments (Figure 218). Larvae of *Mesocia pusilla* and the trosiine from Veracruz, Mexico, have a further modification. In these, the SV row of verrucae is modified into a membranous pad or suction disk, similar to that found on the proleg (Figures 216, 252). This increases the surface area for contact with the substrate and may be of particular utility on smooth surfaces (as discussed in "Function and Adaptation," below).

AIDIDAE Hopp, 1927, new status

ADULT DIAGNOSIS (Figure 48).—Only member of limacodid group with forewing R_1 and R_2 stalked alone near costal margin (Figure 69). Distinguished from Megalopygidae by forewing R_3 and R_4 stalked from R_5 (Figure 69); papillae anales flat and open (Figure 347); without dense pouch of hair-like scales on end of female abdomen; male genitalia with uncus and valvae broad (Figures 352, 353); sensilla trichodea on ventral fifth tarsomere of females without scales intermixed; male antennae bipectinate in basal portion; female antennae filiform; labial palpus porrect and usually three-segmented, longer and less hidden by scales (Figures 54*a,b*). Distinguished from Limacodidae and Dalceridae by presence of chaetosemata; absence of a gnathos (males) (Figures 352, 353); presence of longitudinal depressions on mesonotum (Figure 61); broadly sclerotized mesepimeron (Figure 66). Separated from Limacodidae alone by deeply cleft papillae anales and large secondary accessory glands (females) (Figures 347, 348).

ADULT.—*Head:* Male antenna bipectinate from one-half to two-thirds distance from base (Figure 48); labial palpus either two- or three-segmented (Figures 54*a,b*), porrect, reaching as high as dorsum of eye; galeae and maxillary palpi absent.

Thorax: Forewing cell with stem of medial vein from near base, branched in a V near distal end; R_1 and R_2 stalked in distal one-third of wing beyond discal cell and near costa; R_3 and R_4 stalked from R_5 (Figure 69) (Dyar, 1895c, fig. 21); scales on forewing and legs often spatulate; mid- and hindlegs with 1 short pair of tibial spurs; ventral sensilla trichodea on fifth tarsomere of female without scales interspersed medially (Figures 82–84).

Male genitalia (Figures 352, 353): Uncus gradually tapering from tegumen, apex downcurved, gnathos absent; aedeagus slightly curved, narrowed at tip; valvae broad, entire, and somewhat triangulate with rounded apex; juxtal process (valvella) on each side of aedeagus with upturned, clawed end; vinculum over one-half width of tegumen, saccus weakly developed.

Female genitalia (Figures 347, 348): Papillae anales flattened to posterior, somewhat divided into dorsal and ventral regions, with dorsal portion fused medially; both anterior and posterior apophyses longer than A8; corpus bursae oval and membranous; spermatheca connected with short ductus seminalis near ductus bursae; 2 large sebaceous glands fused at base where connected to common oviduct; secondary accessory glands with 2 medially connected and weakly sclerotized lobes, occupying large proportion of A8; connection of secondary glands to common oviduct unclear, although without external ducts present in Dalceridae.

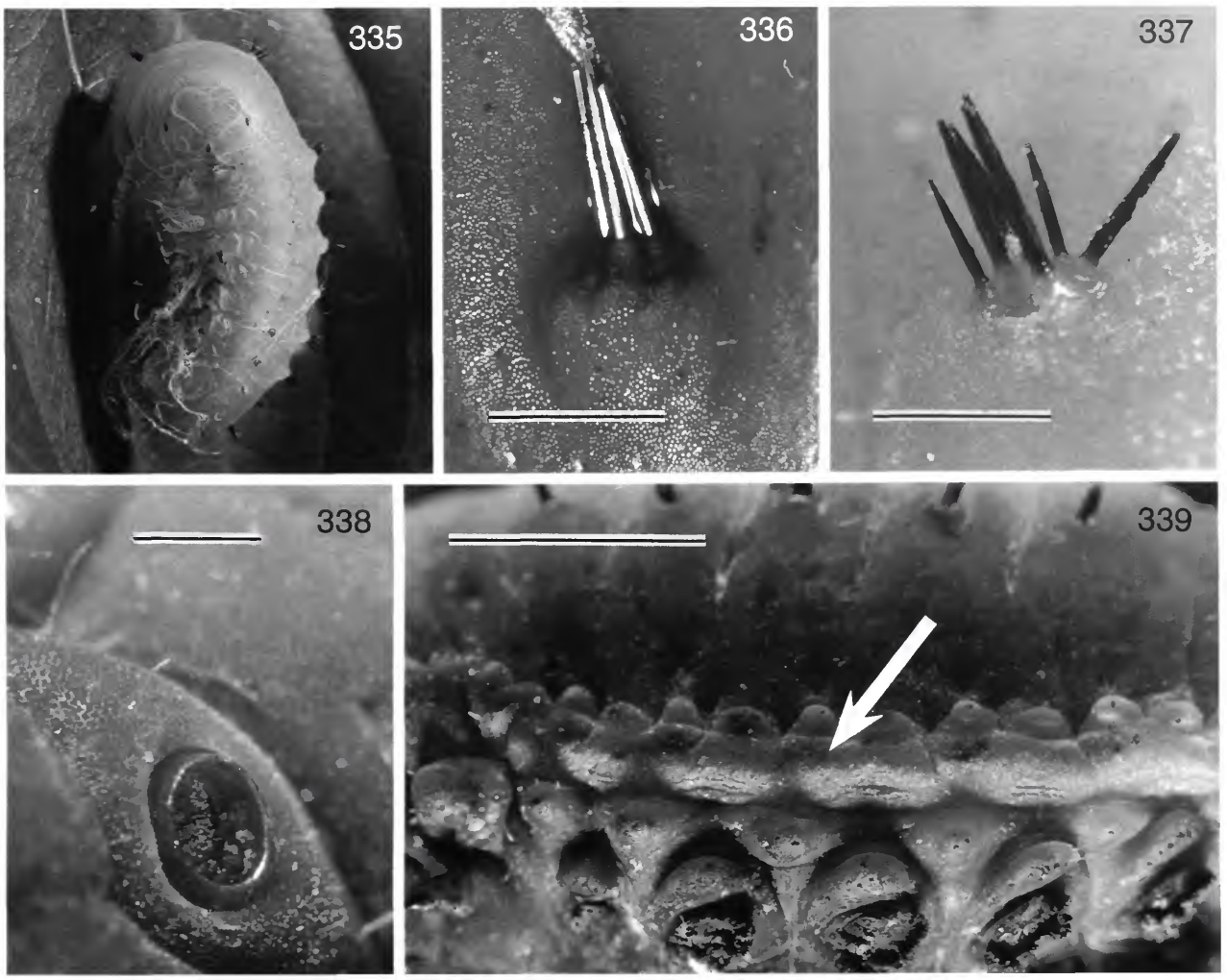
LARVA (Figures 4, 215, 223, 335–344, 407).—*Head:* S1 and S2 present, stemmata as in Megalopygidae except stemmata 1 and 2 have wider gap between them (Figures 120, 121); labrum with stout spines on anterior margin (Figures 129, 130); spinneret tubular, with amorphous tip (Figures 148–151).

Dorsum: Green, without pigment pattern; plumose setae absent, short secondary setae sparse; verrucae with thick, black urticating setae, 5–11 per cluster in D rows A2–A9 and SD rows A2–A7, and fewer urticating setae in D and SD rows on T2; urticating spines sunken and appressed to a common point when in repose (Figure 336), with D row directed ventrad and SD row directed dorsad; spines splayed into rosettes when protruded (Figure 337); spiracle on A1 midway between position of other spiracles and SD row of spines; L1 and L2 setae tactile, borne on 2 warts, equidistant and proximoventral to each abdominal spiracle; L1 and L2 separated by longitudinal ridge and sulcus from row of ventral warts (L3?) found between convex lateral portion of proleg bases (Figures 339, 407).

Ventrum: Length of thoracic legs greater than width of labrum and with unmodified setae (Figures 225–227); prolegs on A2–A7 and A10 as in megalopygids, although without membranous pads or plumose setae (Figures 215, 223); crochets in V-shaped row (50–70 in number) on prolegs A3–A6 (Figures 340–344), linear on A10, and absent on A2 and A7 (Figure 223); anal fork reduced or absent.

PUPA (Figure 312).—Similar to dalcerids except mandibles nearly absent and fractures occur along eye suture during eclosion; frons often with projecting hump; spiracular sensilla absent. Cocoon spun between leaves, with preformed escape hatch, and with 1 or 2 pairs of small, round holes in outer silk mesh, giving appearance of emergence holes of parasitic Hymenoptera (Figures 15, 17).

DISCUSSION.—*Aidos amanda* (Stoll) was "provisionally" placed in Megalopygidae by Dyar (1895c:243–244; as *Brachycodion*), although he was "in doubt whether to refer it to Eucleidae [= Limacodidae]." For the most part, Aidinae has remained in Megalopygidae ever since, although Forbes (1923) considered it a family. Characters of adult Aididae are given by Dyar (1895c), Hopp (1934–1935), and Holloway (1986). The larva (lateral and ventral aspects), cocoon, and pupa were figured and described by Dewitz (1878) based on descriptions and specimens from Gollmer. Descriptions of *Aidos* larvae by Hopp (1934) were less detailed. The cocoons also were described by Klug (1836), Hopp (1930, 1934), and Forbes (1942). Cocoon construction, life history, and host plant information for the Aididae are given in Epstein (1995). Larval



FIGURES 335–339.—Morphology of the larval stage in Aididae (scale length in parentheses) (336, 338 photos by L. Minor-Penland; 337, 339 photos by C. Hansen): 335, *Aidos amanda*, ventral aspect of live larva, note silk on ventrum (photo by K. Sandved). 336–339, *Aidos* sp.: 336, detail of SD verruca, spines in repose (1 mm); 337, detail of verruca, partially opened (1 mm); 338, detail of prothoracic spiracle (1 mm); 339, lateroventral view, anterior to left (arrow points to longitudinal ridge and sulcus) (5 mm).

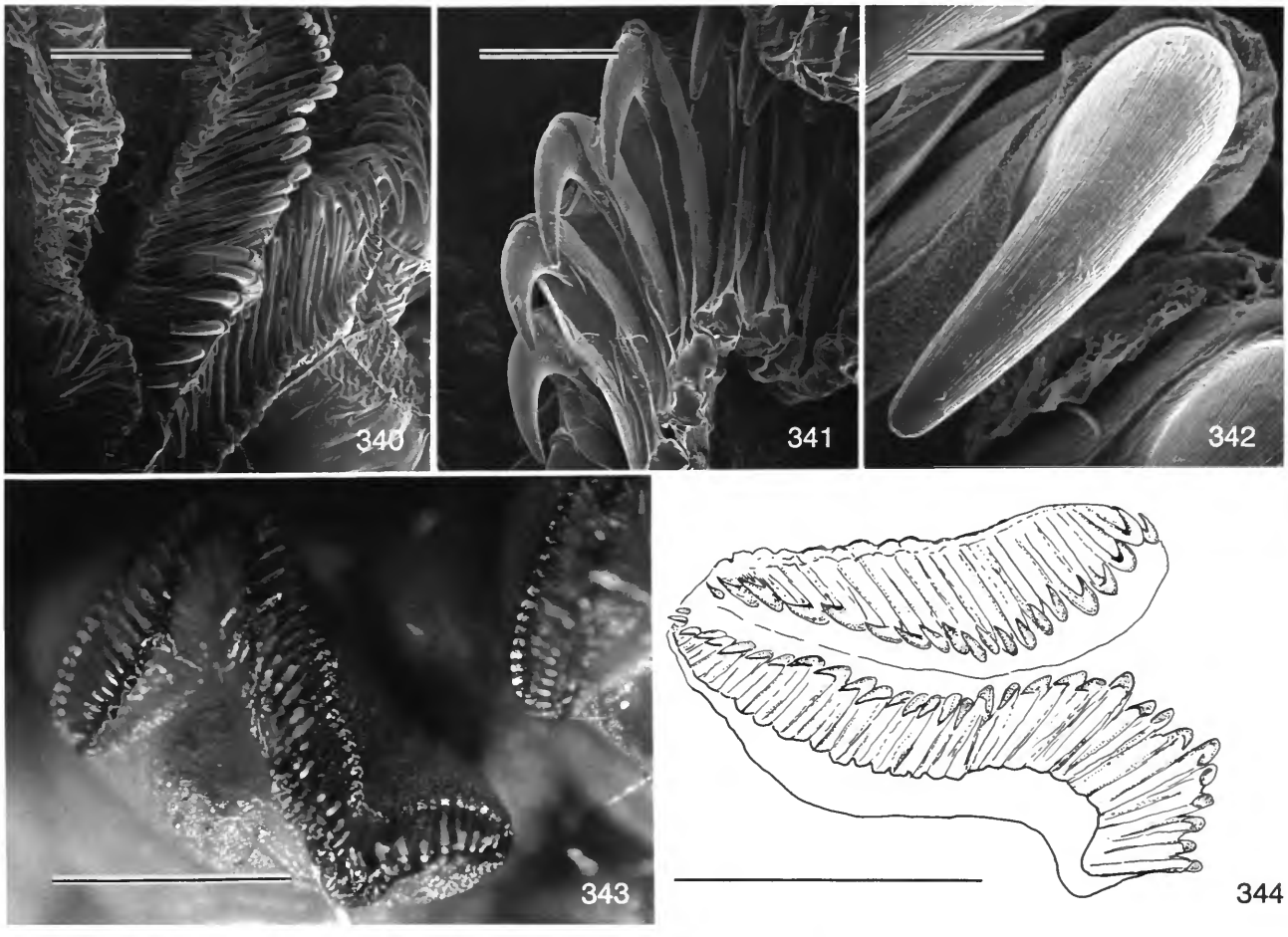
and egg stages described for the Aididae by Hoffmann (1932) (as *Aidos amanda*) were based on a misidentified megalopygine (Epstein 1995).

Aidids have a number of character states not found in either the Megalopygidae or Limacodidae + Dalceridae, some of which are autapomorphic (Table 6) or transitional, and others are plesiomorphic. Placement of "Aidinae" in Megalopygidae would be based on symplesiomorphies with respect to the limacodid group. Examples include the presence of chaetosemata on the adult head and the presence of larval prolegs on A2 and A7. Character states that the Aididae do not share with megalopygids are outlined in the diagnosis above. Holloway (1986) suggested that *Aidos* (Aidinae) either belonged within Limacodidae or was closer to Limacodidae than to Megalopygidae. He based this on characters of the forewing veins (R_3 and R_4 stalked), male genitalia, and female ovipositor lobes. The radial veins and several aspects of the male genitalia, however, are possibly plesiomorphic with respect to the limacodid group, and female genitalic characters suggest a close relationship with Dalceridae (compare Figures 347–350).

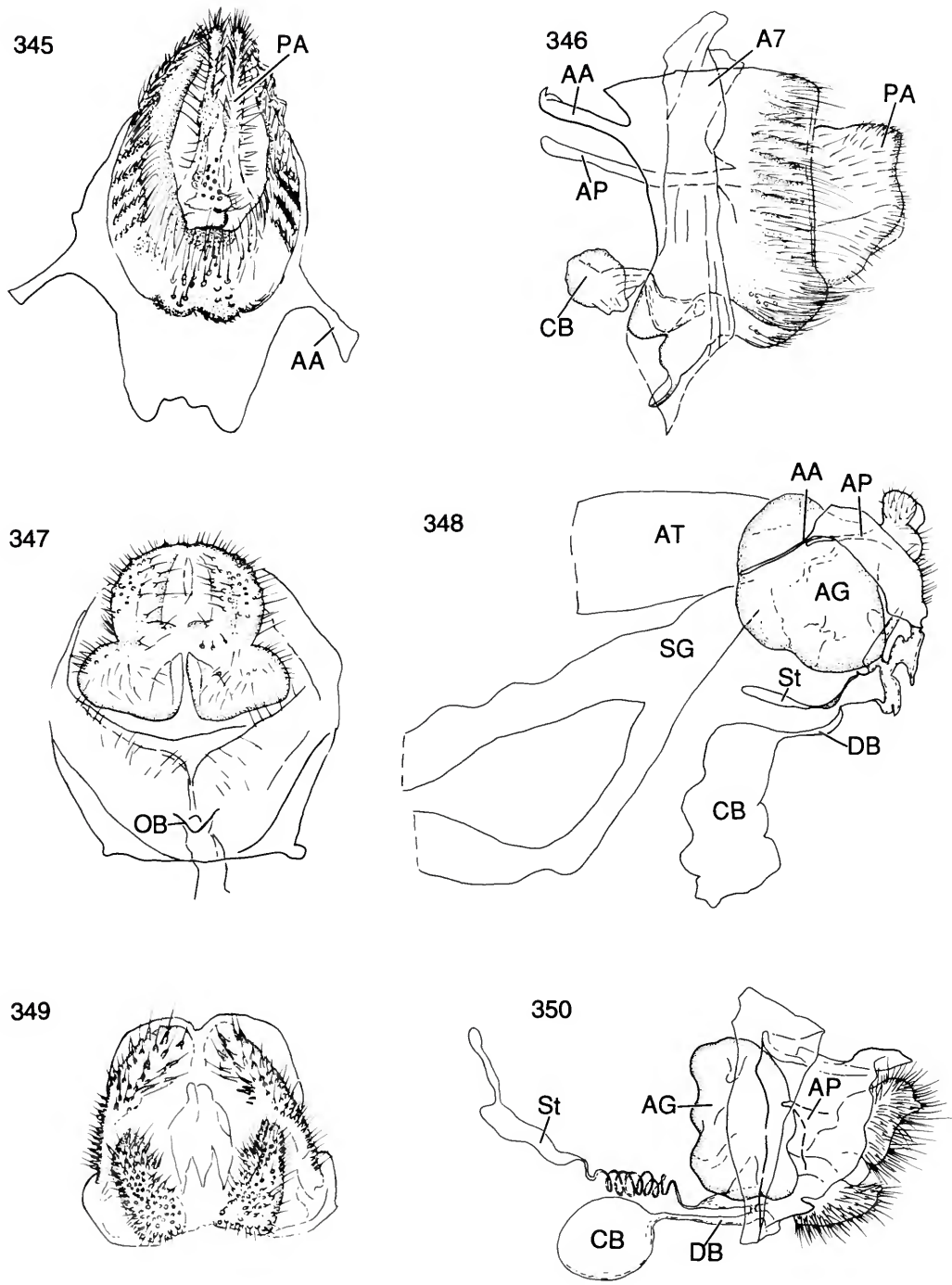
Urticating spines in aidid larvae are borne on a verruca or tubercle and are apparent only when in full defensive display as a rosette (Figure 337). In repose they are somewhat sunken, as noted by Hopp (1934), and appear as if a single spine (Figure 336). A similar condition occurs in Limacodidae in the *Parasa chloris* complex, in New World *Natada* (D.H. Janzen, pers. comm.), and in Australian *Doratifera*. A possible relationship between *Somabrachys* and aidids (as Aidinae) was suggested by Hopp (1934), based on the sunken urticating setae in the larvae; however, the setae in aidids are much more similar to those found in limacodids. The "sunken spines" in *Somabrachys* are actually spiracle-shaped pouches above the spiracles, which contain deciduous pilose material (see Somabrachyidae section, below).

Another larval character found both in the Aididae and in some genera of Limacodidae is the loss of the SD tubercle on A1, with the spiracle located dorsally.

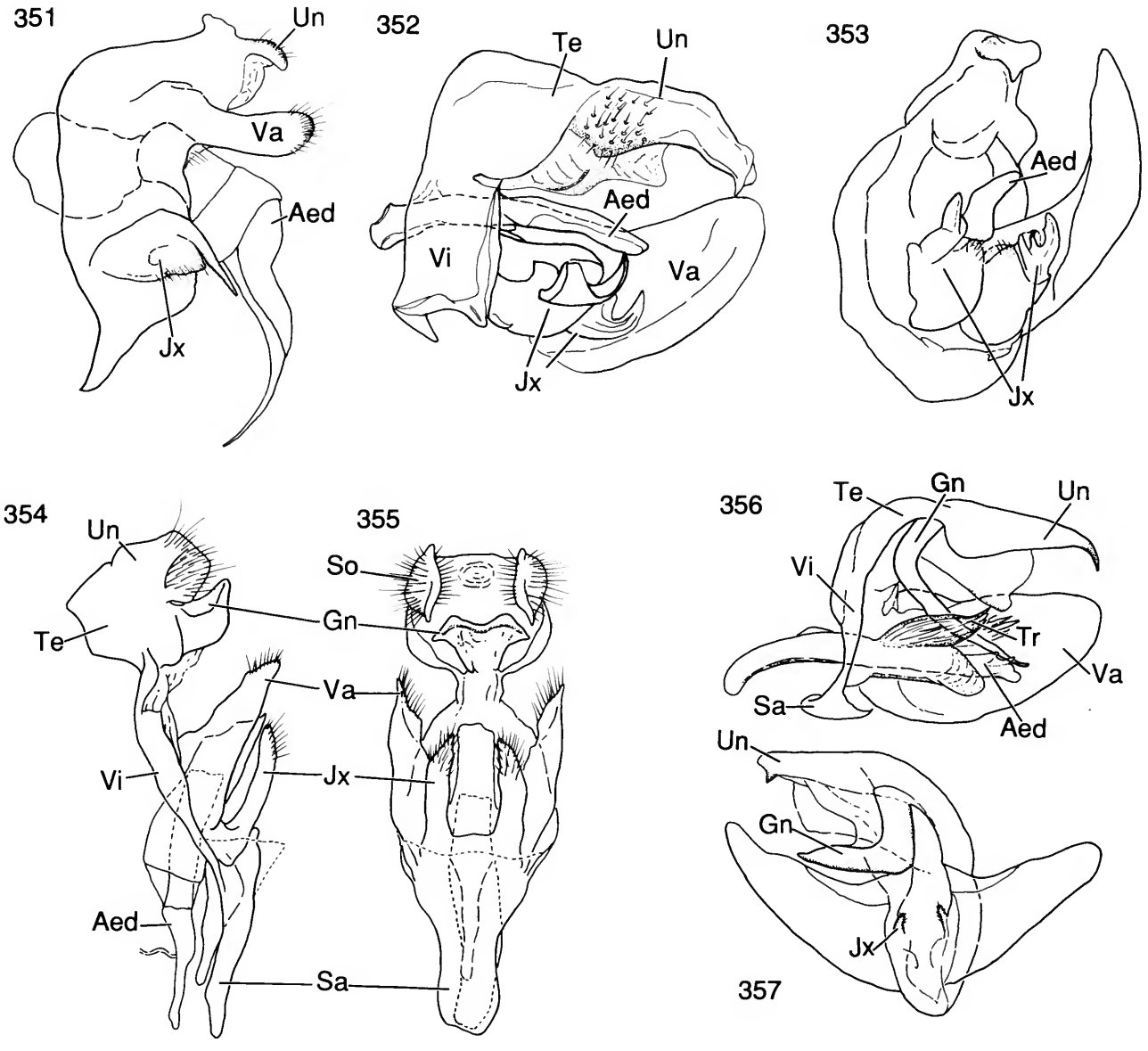
It remains unclear whether the female glands in aidids (Figure 348) are homologous with those found in other Zygaenoidea. Their bilobed appearance most closely resembles the glands of dalcerids (Figure 350) (Miller, 1993) and zygaenids (Naumann, 1988). The female glands in epipyropids and cyclotornids are composed of one part rather than two (Common, 1990). The aidid glands may produce a sticky secretion that coats the eggs, as reported for dalcerids (Miller, 1993). This is suggested by the observation that eggs are sometimes found stuck to the outside of the ovipositor in preserved specimens.



FIGURES 340–344.—Prolegs and crochets in larval Aididae (scale length in parentheses). 340–342, *Aidos* sp. from larval exuvia in cocoon: 340, crochets on 2 adjoining prolegs (0.3 mm); 341, detail of crochets (107 µm); 342, detail of 1 crochet (27 µm). 343, proleg on A3, upper left corner is anterior (1 mm); 344, A4 proleg, *Aidos amanda* (meson to left, 1 mm).



FIGURES 345-350.—Female genitalia in Megalopygidae, Aididae, and Dalceridae. 345, 346, *Megalopyge lanata* (Megalopyginae), Panama: 345, frontal view; 346, lateral view. 347, 348, *Aidos amanda* (Aididae), Brazil: 347, frontal view; 348, lateral view. 349, *Acraga coa* (Dalceridae), Mexico, frontal view; 350, *Dalcerides bicolor* (Dalceridae), lateral view (after Miller, 1994, fig. 252). (AA = anterior apophysis, AG = accessory gland, AP = posterior apophysis, AT = anal tube, A7 = abdominal segment 7, CB = corpus bursae, DB = ductus bursae, OB = ostium bursae, PA = papillae anales, SG = sebaceous gland, St = spermatheca.)



FIGURES 351–357.—Male genitalia of the limacodid group: 351, *Norape corporalis* (Trosiinae), Venezuela, lateral view. 352, 353, *Brachycodilla carmen* (Aididae), Brazil (left valva removed): 352, lateral view; 353, frontal view. 354, 355, *Minacraga aenea* (Dalceridae) (after Miller, 1994, fig. 227): 354, lateral view; 355, ventral view. 356, 357, *Perola* (Limacodidae): 356, *P. producta*, Costa Rica, lateral view (left valva removed); 357, *P. murina*, Brazil, frontolateral view. (Aed = aedeagus, Gn = gnathos, Jx = juxta, Sa = saccus, So = socius, Te = tegumen, Tr = transtilla, Un = uncus, Va = valva, Vi = vinculum.)

DALCERIDAE Dyar, 1898

ADULT DIAGNOSIS (Figure 49).—Forewing R_2 and R_3 stalked or occasionally fused (Figures 72, 74), unique in limacodid group; R_4 and R_5 stalked or fused; wings orange, yellow, or white, sometimes with shiny markings. Chaetosemata absent; labial palpus two-segmented, upturned, reaching vertex (Figures 55, 57*a*); galea and maxillary palpus vestigial, galea basally spinulose (Figures 57*a–c*). Antennae short, about one-fourth length of forewing costa, bipectinate throughout in male, often with scales on apex (Figure 49). Mesepimeron (Figure 65) narrowly sclerotized compared to megalopygids

and aidids. Tibial spurs absent, tarsomeres with large spurs on ventral surface (Figure 89); fifth tarsomere in female covered with scales beneath and with a narrow distal band of sensilla trichodea (Figures 85, 86). Male genitalia with uncus and valvae reduced; socii and gnathos present; juxtal arms often present; saccus narrow, extending cephalad (Figures 354–355). Female genitalia with papillae anales deeply cleft; accessory glands large, with external ducts (Figures 349, 350).

LARVA (Figures 3, 177, 180).—*Head:* Stemma 5 disjunct ventrally, more distant than width of 1 stemma from stemma 4; only S1 seta present, located proximate to stemmata 1–3 (Figures 122, 123); labrum with dense anterior bristles on mesal portion only (Figures 134, 135). Spinneret wider at apex than at base (Figures 152–156); in post-first instars, a brush-like comb along apical margin, with deeply divided bristles (Figures 152–155) and with dorsal surface reduced medially, revealing a narrow, longitudinal silk pore (Figure 154).

Dorsum: Prothoracic shield translucent, with tactile primary setae present; XD, D, SD, and L all hair-like at middle to late instars (the cuticle was too distorted to observe setae, except L in first instars); 2 (first instar) or 3 (later instars) L setae below spiracle (Figures 186, 187). D and SD setal rows consist of thick primary setae covered with gelatinous warts on T2, T3, and A1–A9; L seta on T2 and T3 covered with gelatinous wart (Figures 177, 180); often with brightly colored pigmented patterns on cuticle beneath gelatinous warts. T2 with D1 and D2, and SD1 and SD2, each in horizontal rows, with L1 below; tactile setae MSD1 and MSD2 anterior to SD setae. T3 with setae as on T2 except groups vertical, 1 SD present, and MSD setae absent. A1–A8 with D1, D2, and SD1 setae (also with SD2 in late instars); A9 with 2 D and 1 SD setae. Three tactile setae present below gelatinous setae on T2 and T3, perhaps representing 2 SV setae and 1 MV seta. Lateral abdominal region between gelatinous setae and ventrum spinulate; spiracles closer to ventrum than in Limacodidae; 2 hair-like L setae posterior to each spiracle, and 1 MSD2 seta anterodorsal to spiracles fungiform (first instars) (Figures 208, 209) or hair-like (later instars) (Figures 177, 180).

Ventrum: Thoracic legs small, about equal in length to width of labrum (Figure 112); axial seta inside pretarsal claw hair-like (Figure 231); V1 seta mesal of thoracic legs fungiform (Figure 243). Ventral surface of thorax and A1–A9 with cuticle translucent and flexible throughout, except narrow band of spinulose cuticle on anterior portion of T1 (Figure 243); shallow suckers on A1–A8 in later instars (Figures 261, 408), with flexible cuticle lateral to suckers as in limacodids. Ventral fungiform setae in horizontal row of 3, with SV1, SV2, and V1 from lateral margin to meson (Figure 262). Crochets (Figures 261, 264) on A3–A6 small, few in number (up to 17), arranged in a crescent between SV2 and V1 setae (Figure 263); absent in early instars (Figures 224, 262). Additional sets of crochets sometimes added in late instars on A2 and A7 (e.g., *Dalcerides ingenita*). Anal proleg (A10) vestigial, spinulose, and without crochets; with 8 primary setae, 6 on lateral lobe and 2 on mesal lobe (Figure 276); frass-flipping setae either absent or present on dorsomesal portion near the anus (Figures 286, 289).

PUPA (Figures 297, 298).—Eye with sculptured flange that remains connected to eyepiece at eclosion (Figure 303). Labial palpi one-quarter length of head, maxilla not reaching eye flange (Figure 315). Four (2 groups of 2) or 6 (2 groups of 3) setae present on frons (Figure 325). Cremaster hooks present (Figures 309, 310); rows of spinules present on anterodorsal portion of segments A2–A6 (Figure 311).

DISCUSSION.—Adult characters of the Dalceridae were given by Miller (1994). The larva has been described by Dyar (1925), Hopp (1928), and Stehr and McFarland (1985, 1987). Dalceridae has been previously reported as being closely allied to Epipyropidae (Jordan, 1928), Limacodidae (Dyar, 1925), and Megalopygidae (Minet, 1986). Since achieving family status, Dalceridae has been cited no fewer than six times as a subfamily of Limacodidae (Miller, 1994), including citations by Janse (1925), Hopp (1928), and Zerny and Beier (1936). Forbes (1942:392–393) considered the larva, cocoon, and forewing accessory cell of dalcerids to be primitive for Zygaenoidea, suggesting that dalcerids were a lineage separate from both limacodids and megalopygids. The division of Dalceridae into the subfamilies Dalcerinae and Acraginae by Orfila (1961) was confirmed by Miller (1994).

Monophyly of the Limacodidae and Dalceridae is supported by a suite of larval synapomorphies (Table 6). New character information for primitive limacodid genera, such as *Pantoctaenia* and *Crothaema,* may eventually support either the inclusion of Dalceridae within Limacodidae or an expanded concept of Dalceridae. Autapomorphies (Table 6) support the Dalceridae as a monophyletic group, although modifications in male genitalia and in forewing radial veins, and the loss of tibial spurs, could have been derived within Limacodidae. The Dalceridae, however, do have putative plesiomorphies in the immature stages that are not observed in the Limacodidae (+ Chrysopolomidae, *Pantoctaenia, Crothaema*), including (1) a disjunct stemma 5 in the larva (Figure 122); (2) long setae on the larval thoracic legs (Figure 231); (3) a pupal labial palpus without contiguous maxillary lobes (Figure 315); and (4) setae on the pupal frons (Figure 325). Although present in the Zygaenidae (e.g., *Onceropyga anelia* Turner, see Common, 1990), the setae on the pupal frons have not been observed elsewhere in the limacodid group. Female characters shared with aidids include cleft papillae anales and a large female accessory gland (compare Figures 347, 348 with 349, 350). These may be considered synapomorphies, although the accessory gland may also be plesiomorphic if it is homologous with the gland found in Zygaenidae.

I concur with Forbes (1942) and Miller (1994) that the forewing accessory cell (areole) is primitive (plesiomorphic) in Dalceridae (Figure 74). It appears to have been independently lost or fused in the subfamily Dalcerinae (Figure 72) (Miller, 1994) and in other members of the limacodid group. The

posterior vein of the areole is traditionally considered to be a radial vein (Miller, 1994), with the other solitary cell vein being medial. Among terminal taxa of the cladogram presented (Figure 326), the radial vein in the discal cell has not been found in the Aididae or Megalopygidae. This radial vein occurs in some Chrysopolominae (sensu nova) (Ectropinae of Hering, 1937) and in other zygaenoids including the Epipyropidae and some Zygaenidae (Common, 1990).

Based on the phylogenetic analysis and new character information presented herein, I disagree with Forbes's (1942) interpretation that the larva and cocoon of the Dalceridae are primitive within the limacodid group. I consider the inner chamber of dalcerid cocoons to be autapomorphic in the Zygaenoidea, supported by its unique function in the removal of the gelatinous material from the prepupa (see "Biology," above). It is unclear which aspects of the larva Forbes considered to be primitive, although my phylogenetic evidence does not support his contention. I discuss the polarity of dalcerid larval characters in the body setae and the prolegs sections, below.

Electron micrographs of early instars of *Dalcerides ingenita* and of a dalcerid species from Ecuador (CMNH) (Figures 224, 262) did not reveal crochets. This confirms reports that crochets do not occur in early-instar dalcerids (Stehr and McFarland, 1985, 1987). Crochets, reported on segments A2 and A7 in late instars of *D. ingenita* and *Acraga coa* (Stehr and McFarland, 1985), have not been found in late instars of other dalcerid species examined thus far. These include larval specimens in the *Acraga infusa* complex from Colombia (Genty collection), *D. tijucana*, and several undetermined specimens from Mexico, Brazil, and Peru.

The homology of male genitalic structures in Dalceridae proposed by Miller (1994) is supported by observations of genitalic structures in the Megalopygidae, Aididae, and Limacodidae. In Dalceridae, *Minacraga* (Figure 354, 355) and *Dalcera* species have "juxtal processes" and "valvae" in similar position and appearance to those found in the Megalopygidae (Figure 351) and Aididae (Figures 352, 353). The gnathos in the Dalceridae appears to be homologous with the structure in the Limacodidae (Figures 356, 357).

LIMACODIDAE Duponchel, 1844

ADULT DIAGNOSIS (Figures 51, 52).—Forewing R_3 and R_4 stalked (Figures 71, 73), rarely fused, branching from R_2, R_5, or in-between; R_1 and R_2 separate, not stalked as in Aididae. Only limacodid-group family with hindwing Rs and M_1 stalked from near the end of the discal cell or beyond (Figure 73) (found in majority of species). Chaetosemata absent; labial palpus three-segmented, often relatively long and upturned (Figures 56*a,b*); galea present and smooth compared to Dalceridae (Figures 58, 59), or absent; maxillary palpus commonly one-segmented (Figures 58, 59). Male antennae ranging from bipectinate to filiform. Hindtibia with 1 or 2 pairs of spurs; fifth tarsomere of female usually with dense mat of ventral sensilla trichodea on recessed pad without scales interspersed (Figures 99–103). Male genitalia with well-developed gnathos, uncus, and valvae (Figures 356, 357). Female genitalia usually with large, flat ovipositer lobes, disk shaped or emarginate on lateral margin, not deeply cleft as in dalcerids and aidids (Figure 362); digitate and membranous lateral lobes often present on A8, dorsal to anterior apophyses (Figure 362); corpus bursae with signum present or absent.

LARVA (Figures 6, 7).—*Head:* Stemmata 1–4 nearly evenly spaced; stemma 5 slightly more removed from stemma 4 than stemmata 1–4 are from each other; stemma 6 most isolated, equidistant to stemmata 1 or 5; only S1 seta present, proximate to stemmata 1–4 (Figures 126–128). Labrum often with a large number of bristles covering anterior margin (Figures 138–141), more extensive than in related families. Spinneret shape variable, usually widest at apex (Figures 158–162, 367–370), although sometimes tapering distally (post-first instar) (Figures 371–384) or narrow and more tubular (first instar) (Figures 389–392); dorsal surface with (Figure 385) or without longitudinal striae (Figure 367).

Dorsum (first instar): D and SD setal groups as tubercles or warts on T2, T3, and A1–A9 (Figures 170–176, 181, 393). L setae paired on T1, proximate to spiracle (Figure 183–185); L on T2 and on T3 as an individual tubercle (Figure 178, 179, 181), fused with SD row, or absent.

Dorsum (post-first instar): Larva with spiny scoli, hairy tubercles, or verrucae (Figures 402, 405), or larva relatively smooth, without tubercles, and with simple setae; rarely with gelatinous warts similar to those of Dalceridae. L setae ventral to spiracles on abdomen (Figures 204–207, 210–214), with ventral seta L2 sometimes modified to fungiform (Figure 205) and dorsal L1 rarely spatulate (Figure 204); L setae on relatively stiff longitudinal ridge (= flange of Holloway, 1986) bordering flexible ventral surface.

Ventrum: Pretarsal claw on thoracic legs with axial seta directly under hooked portion, seta hair-like and somewhat closer to tip than to base (Figure 234) as in Dalceridae, or reduced (Figure 233) or vestigial (Figure 239). Paired setae on each side of thoracic legs shorter than in Dalceridae (compare Figures 231 and 232, 233); tips on longest setae blunt or capitate (Figure 273); setae longest on pretarsus, varying from roughly equal to length of pretarsal claw (Figures 232, 234) to reduced and often fungiform (Figures 237–239). Crochets absent in first instars (Figures 266–270, 348), present only in late instar *Pantoctaenia* on A2–A7 and A10 (Figures 358–360). Ventral cuticle flexible and translucent, as in dalcerids, with oval suckers on segments A1–A8, usually more defined in later instars (Figure 222), and with flexible region between lateral margin of suckers and flange below spiracles (Figure 409). Anal proleg as in dalcerids except crochets present in late instar *Pantoctaenia;* usually spinulate and lobate with 5 or 6 primary setae on lateral lobe and 2 primary setae on mesal lobe (Figure 277); frass-flipping setae occurring singly or in small

groups (Figures 277, 288, 290), or absent (Figures 295, 296). Anal plate with D1, D2, SD1, and SD2 setae present; anal comb absent (Figure 277).

PUPA (Figures 314, 316, 318, 319).—Labial palpus long, often one-half length of head, with parallel maxillary lobe adjoining it laterally (Figures 316, 318). Eyepiece breaks at suture during eclosion (Figures 304, 305) (compare Chrysopolominae and Dalceridae). Maxilla with (Figure 316) or without (Figure 318) a lateral extension; when present extension holds foreleg beneath at femur-tibia junction. Cremaster hooks present (Figure 308) or absent.

DISCUSSION.—Relationships with other family groups are reviewed in discussions of the Dalceridae and Aididae above. The Limacodidae have been divided into suprageneric groups although these have not been widely accepted, due at least in part to the broad geographic range of this family. Taxa in limacodid generic complexes mentioned below are given in Table 3.

Dyar's (1899a) classification of New York limacodids was based on larval characters. He considered primitive limacodids to have three rows of tubercles on thoracic segments in the first instars, more closely matching the megalopygid and zygaenid (= pyromorphid) condition. Dyar regarded the three-rowed *Phobetron* complex ("Tropic hairy" larvae) as both the oldest group and the group that gave rise to the two-rowed *Parasa* and *Natada* complexes ("Tropic spined" larvae). Groups with three rows of tubercles in first instars and without spiny tubercles in late instars, *Prolimacodes* ("Tropic smooth" larvae) and *Apoda* ("Temperate smooth" larvae) complexes, constituted the other main branch.

Tutt (1899) and Forbes (1923) gave tribal names to Dyar's lineages. *Crothaema* was given monotypic subfamily status by Hering (1955), but this was not accepted by Janse (1964). Holloway (1986) suggested possible groupings based on the signum of the corpus bursae in females.

Characters of *Pantoctaenia* and *Crothaema*, plesiomorphic based on the phylogenetic evidence presented above, suggest that these are the most primitive limacodids examined. The presence of crochets on A2–A7 and on A10 in *Pantoctaenia gemmans* (Figures 358–360) is a condition previously found only in some megalopygids. As in dalcerids, these crochets do not appear until after the first instar; this follows the reasonable assumption that the first instar of *P. gemmans* is like that of *P. prasina* (i.e., lacks crochets). The close relationship between these two species is supported by adult features given by Janse (1964). The flattened end of the cocoon in *Crothaema* suggests a hatch, a condition not reported in other limacodids (cocoons in *Pantoctaenia* have not yet been examined). Another symplesiomorphy of *Pantoctaenia*/*Crothaema* + Dalceridae is the condition of the fifth tarsomere in females, where the sensilla trichodea are confined primarily to the distal portion (Figures 93–95). The ovoid egg in *Pantoctaenia* also appears to be plesiomorphic, resembling that of megalopygids and dalcerids rather than the flat, scale-like eggs of limacodids.

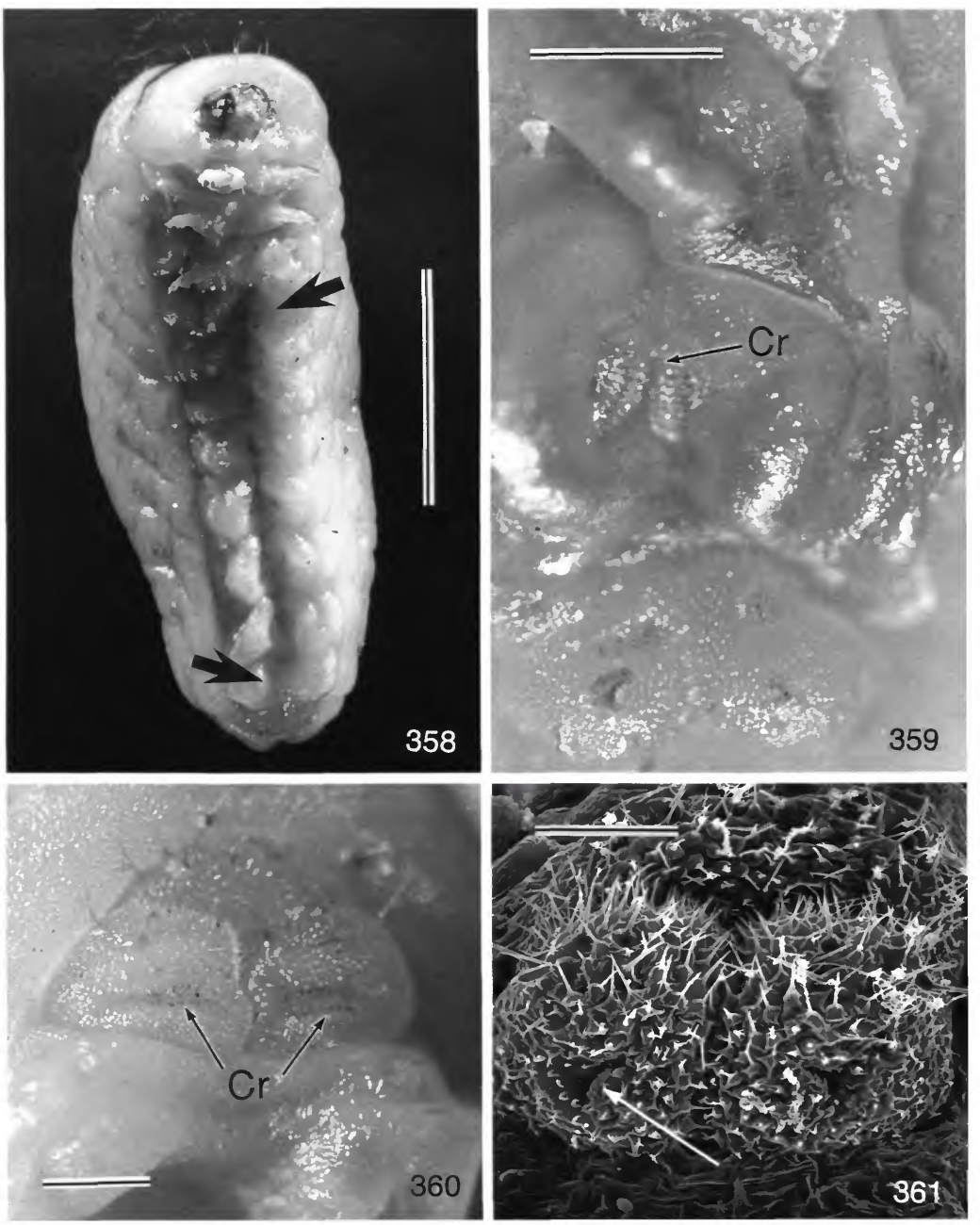
Some larval plesiomorphies found in *Pantoctaenia* and *Crothaema* occur in other genera as well. These include the presence of D1, D2, SD1, SD2, and L1 setae (tubercles) on T2 in the *Apoda* and *Prolimacodes* complexes (Figures 178, 179), as well as the presence of two D and one SD tubercles on the abdomen in these complexes and in *Belippa* (Figure 188) (discussed further in "Homology and Evolution of Larval Body Setae," below). Also potentially plesiomorphic is the smooth anterior margin of the labrum (Figure 136), which occurs in *Apoda*, *Pantoctaenia*, and *Chrysopoloma* (see below); as in dalcerids, epipharyngeal spinules of *Crothaema* are visible from above only in the medial region.

Comstock (1918) considered the presence of a crossvein connecting Rs and M_1 at the end of the hindwing discal cell (e.g., *Apoda*) to be the primitive condition for limacodids (Figure 71), and he considered the stalked condition of $Rs + M_1$ (e.g., *Adoneta*) to be derived (Figure 73). This is supported by the presence of the crossvein in genera with primitive larvae, such as *Pantoctaenia* and *Crothaema* (see Janse, 1964), the *Apoda* complex (*Packardia*, see Comstock, 1918), *Pseudonapaea* (Common, 1990), and *Demonarosa* (Holloway, 1986). The presence of a bisignate corpus bursae in *Pantoctaenia* and *Crothaema* (Janse, 1964) suggests that other character states of the signum (Holloway, 1986) may be derived from this condition.

The digitate maxillary extensions of the pupa represent a putative synapomorphy for a lineage comprising some species in the *Apoda* complex (Chapman, 1893; Packard, 1895a) and *Chrysopoloma* (Figure 317), as well as complexes with spiny larvae, such as the *Parasa* complex (Figure 316) (Packard, 1895a; Mosher, 1916) and *Natada* complex. These maxillary extensions do not occur in plesiomorphic groups, such as *Crothaema*, the *Prolimacodes* complex (Figure 314) (Mosher, 1916), or the *Phobetron* complex. This is contrary to Dyar's genealogy (1899a), in which the genera with spiny larvae form a lineage with the *Phobetron* complex, and the genera with smooth larvae form the other major lineage. Independent losses of maxillary extensions appear to have occurred in two lineages of spiny limacodids, the *Natada* complex (e.g., *Euprosterna*, Figure 318) and the *Parasa* complex (e.g., *Monoleuca*, Figure 319).

Because of their position, the homology of limacodid juxtal lobes (Figure 357) or processes is less certain than the homology of those of aidids, dalcerids, and megalopygids. Juxtal homologies, however, may be easier to defend in limacodid lineages that have species with processes in both transtillar and juxtal regions (e.g., *Perola* complex, Figures 356, 357).

Greater species richness in the Limacodidae appears to be correlated with greater morphological diversity compared to other families in the limacodid group. This diversity of characters is probably due in large part to radiation into a greater number of lineages, which of course increases with the inclusion of Chrysopolomidae. The discovery of suites of



FIGURES 358–361.—Crochets in *Pantoctaenia* (Limacodidae) (scale length in parentheses). 358–360, *Pantoctaenia gemmans*, ultimate instar: 358, ventral view, arrows point to suckers on A1 and A8 (5 mm) (photo by C. Hansen); 359, crochets mesal of sucker on A7, A10 proleg below (1 mm); 360, crochets on A10 (1 mm) (359, 360, photos by L. Minor-Penland). 361, *Pantoctaenia prasina*, 1st instar (arrow points to position on A10 where crochets are expressed in late instar *P. gemmans* (50 μm). (Cr = crochets.)

plesiomorphies in *Pantoctaenia* illustrates that a number of character states once believed to be the ground plan of Limacodidae have been derived within the family. The future challenge in arriving at a phylogenetic hypothesis and higher classification of Limacodidae will be to adequately sample the diversity within its lineages.

CHRYSOPOLOMINAE Aurivillius, 1895, new status

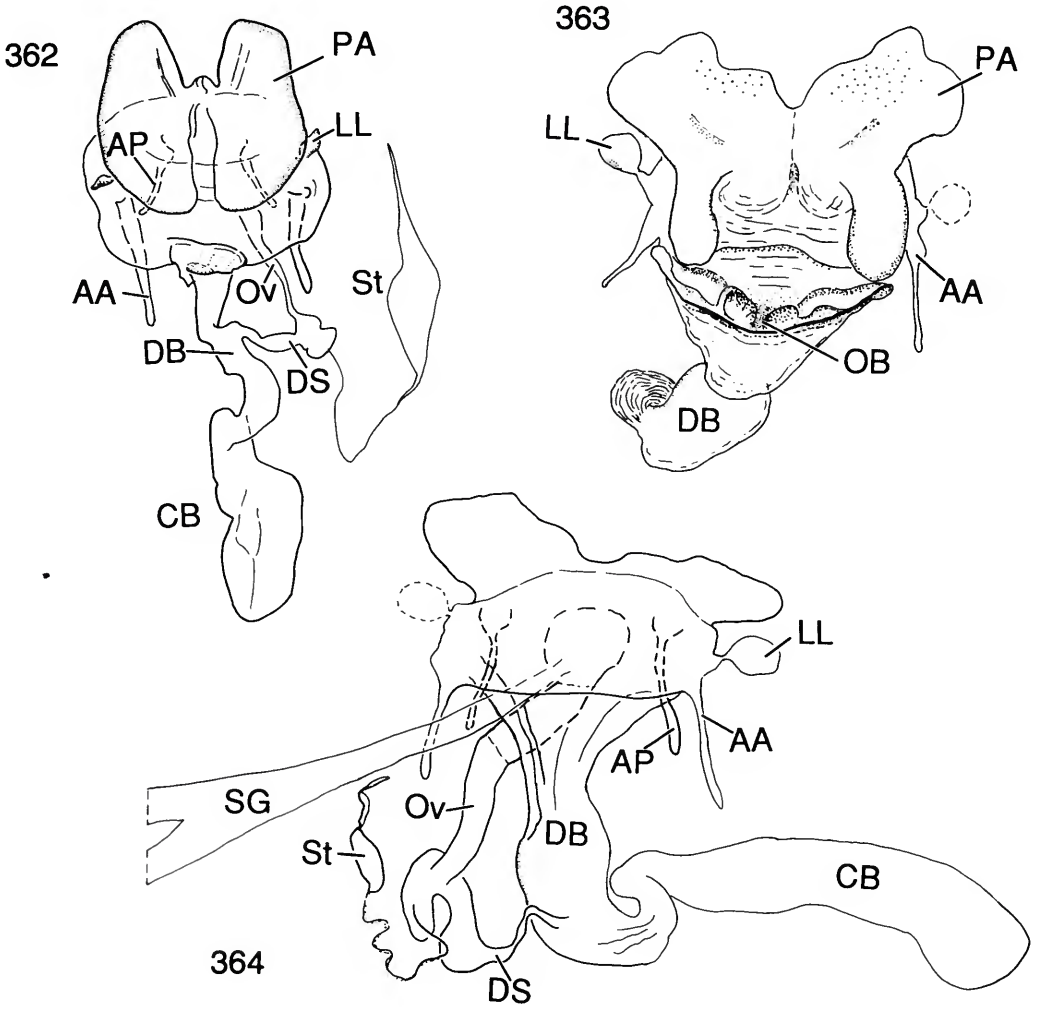
ADULT DIAGNOSIS (Figure 50).—Forewing R_3 and R_4 sometimes unstalked, branching from R_2. Male antennae bipectinate to tip. Reduced sclerites in mesepimeron as in other Limacodidae and in Dalceridae. Distinguished from other limacodids by the absence of gnathos (males) and frenulum. Female with lateral lobes on A8, as in Limacodidae, and concave lateral margins of papillae anales (Figures 363, 364). Female fifth tarsomere with recessed pad similar to but more ovoid than that of other Limacodidae (Figures 96–98).

LARVA (Figure 5).—*Head:* One S1 seta on head (Figures 111, 125), as in limacodids and dalcerids; stemmata arrangement similar to limacodids. Labrum without multiple spines on anterior margin commonly found in Limacodidae (Figure 137).

Dorsum: Spinulate, green or pink, with long, black, hair-like setae having white tips, 1 seta in D row per segment, and 2 L setae below spiracles; length of each seta over one-half body width. Spinules evenly distributed over dorsum, longer proximate to spiracles.

Ventrum: Crochets absent; thoracic legs as in Limacodidae.

PUPA (Figure 317).—Maxillary lobe parallel to and adjoining labial palpus, lateral extension of maxilla adjacent to eye,



FIGURES 362–364.—Female genitalia of Limacodidae and Chrysopolominae: 362, *Perola producta* (Limacodidae), Costa Rica, frontal view. 363, 364, *Achrocerides theorini* (Chrysopolominae), Cameroon: 363, frontal view; 364, viewed from behind. (AA = anterior apophysis, AP = posterior apophysis, CB = corpus bursae, DB = ductus bursae, DS = ductus seminalis, LL = lateral lobe, OB = ostium bursae, Ov = common oviduct, PA = papillae anales, SG = sebaceous gland, St = spermatheca.)

both digitate; mandibles very small. Sculptured eyepiece intact on exuvia after eclosion, as in Dalceridae. Cocoon smooth, oval, and hard, with circular lid, as in Limacodidae; constructed just below ground surface (N. Duke, pers. comm.).

DISCUSSION.—Adult characters of the Chrysopolominae (sensu nova) were described by Hering (1937, 1961). Pinhey (1975:50–51) described the larva as "like Limacodidae but ... have no spines." He described the larva of *Chrysopoloma varia flaviceps* as "bright pink, short and squat, resembling ... jujubes ... feeds on *Gymnosporia*." N. Duke (pers. comm.) found a green fourth instar of *Chrysopoloma similis* (Figure 5) on *Maytenus heterophylla* (Celastraceae) near Pietersburg, northern Transvaal, South Africa (January, 1988).

Subfamily placement should be viewed as preliminary because definitive status must await a higher classification for the Limacodidae. Chrysopolominae (sensu nova) has been considered to be closely allied with Limacodidae, a member of the same superfamily (Zerny and Beyer, 1936), or unrelated (Börner, 1939). Likely synapomorphies with Limacodidae or with lineages presently in the family include (1) absence of larval crochets (except *Pantoctaenia*); (2) stemma 5 proximate to stemma 4 (Figures 111, 125); (3) a hard, oval cocoon; (4) lateral extension of the pupal maxilla (Figure 317); (5) portion of pupal maxilla contiguous with labial palpus; (6) lateral lobes on adult female A8 (Figures 363, 364); and (7) pads with sensilla trichodea on the fifth tarsomere in females (Figures 96–98).

The synapomorphies above occur in limacodid genera with smooth larvae, including the *Apoda* complex, and in spiny larvae, including the *Parasa* and *Natada* complexes. Synapomorphies 4–7 are not found in limacodid genera presumed to be primitive (e.g., *Pantoctaenia, Crothaema*) or in the Dalceridae; synapomorphies 4 and 6 are absent in the *Phobetron* complex, and synapomorphy 4 is absent in the *Prolimacodes* complex. Thus, "smooth-larva" genera in the *Apoda* complex appear to have closer affinity to chrysopolomines than do other genera with smooth larvae (e.g., *Prolimacodes* complex, *Crothaema*). Potential synapomorphies with Limacodidae + Dalceridae include the presence of S1 setae only in larvae (Figure 125) and the narrow, sclerotized band on the adult mesepimeron.

The absence of the frenulum and gnathos in chrysopolomines (Hering, 1937) appears to be autapomorphic with respect to limacodids. To my knowledge, the only plesiomorphic character in chrysopolomines compared to limacodids is the presence of a radial vein, forming an elongate accessory cell, within the forewing discal cell. The presence of a smooth larval anterior labral margin (Figure 137), rather than one with multiple spines, also occurs in *Pantoctaenia* and *Apoda*.

Brock (1971:53) hypothesized that the forewing radial vein arrangement of R_3 and R_4 branched from R_2 in chrysopolomids and in some limacodids is "advanced." This is supported by my cladogram and by the condition in "primitive" limacodids. His one example, *Strigivenifera* (= *Chrysopoloma*) *venata*, which has R_3 and R_4 unstalked, differs from the stalked condition in *Chrysopolomides nivea* (Aurivillius) and *Chrysopoloma rudis* (Walker), figured in Hering (1937, figs. 1, 2). Further study will be required to determine which condition of the two veins represents the ground plan of Chrysopolominae.

SOMABRACHYIDAE Hampson, 1920

ADULT DIAGNOSIS (Figure 47).—Forewing R_{1-5} with 2 veins fused; arise at upper distal part of discal cell with middle 2 veins stalked; females winged (*Psycharium*) or apterous (*Somabrachys*). Hindwing $Sc + R_1$ fused with discal cell. Chaetosemata form distinct band, more developed than in megalopygids and aidids. Sculptured process (*Somabrachys*) or less developed wrinkles (*Psycharium*) present on frons; epiphysis present (*Somabrachys*) or absent (*Psycharium*).

LARVA.—*Head:* Stemma 5 disjunct, similar to Megalopygidae and Aididae; 2 S setae present (Figure 118); spinneret (Figure 144) and labrum as in Megalopygidae.

Dorsum (early instar *Psycharium*): D verrucae on T2, T3, and A1–A9, with urticating setae only (Figure 167); solitary seta (SD) proximodorsal to spiracle; L and SV verrucae with tactile setae.

Dorsum (late instar *Psycharium*): T1 and A10 with D and SD verrucae continuous and covered with entirely tactile setae; T2 and A9 with small pair of D verrucae with short urticating setae and few tactile setae; T3 and A1–A8 with 1 large D verruca on dorsum, consisting of only urticating setae in rosette. A1–A8 SD verrucae reduced to few urticating and tactile setae anterior and proximate to spiracles; A9 SD verruca either absent or merged with L verruca; indistinct patches of flat, scale-like setae on anterior margin of T3 and ventral to D verrucae on A1–A8, with smaller group posterior to D setae on T2; hair-like setae ventral of D verrucae, extending to L verrucae along posterior margin of T3 and A1–A8. Dense patch of tiny detachable spinules on A1, between spiracle and D verruca, not easily distinguished from pigmented region in same position on other segments. L verrucae proximoventral to spiracle with short urticating setae and long tactile setae; SV verrucae on lateral portion of proleg bases and lateral to thoracic legs with only tactile setae.

Dorsum (late instar *Somabrachys*): All verrucae, T1–T3, and A1–A9 with urticating and tactile setae; T2 and T3 with D1, D2, SD, L, and SV verrucae; A1–A8 each with 1 D and 1 SD verruca and a shallow, recessed pouch, dorsoposterior to spiracle and SD verruca, lined with thin, detachable hair-like scales (detachable scales also line spiracles); A1–A9 with 2 L verrucae and 1 SV verruca.

Ventrum: Thoracic legs large in relation to prolegs, especially in *Psycharium* (Figure 217). Two spatulate setae near claw on thoracic legs (Figure 230) (early instar *Psycharium*). Prolegs without membranous pads, segments A2 and A7

without crochets (Figures 249, 250); mesoseries in later instars divided into 2 parts, anterior set with fewer crochets. Early instar prolegs with 2 spatulate setae on anterior margin (*Psycharium*) (Figures 249–251). Late instar prolegs with up to 7 stout, spinose SV setae anterolateral to crochets (*Psycharium*) or with normal hair-like setae lateral to crochets (*Sombrachys*). Anal plate equal to A9 above, with numerous tactile setae. Anal comb present in *Psycharium* (Figures 279, 280, 282) and *Somabrachys* (Jordan, 1909).

DISCUSSION.—The relationship between *Somabrachys* and *Psycharium*, as well as the relationships between these genera and the limacodid group, are still not well understood; however, revisionary work on Somabrachyidae is now in progress (H. Geertsema, pers. comm.).

The placement of Somabrachyidae in Megalopygidae is problematic because most characters shared between the two groups, such as larval prolegs on A2–A7, are shared with the entire limacodid group. Other examples include (1) a disjunct stemma 5, which occurs in all the families except Limacodidae, although to a lesser degree in Dalceridae; and (2) spatulate ventral setae on the tarsus and prolegs, found in first-instar *Psycharium* (Figures 230, 250), megalopygids (Figure 260), and zygaenids (Figure 247) (Stehr, 1987c). The presence of deciduous scales on the end of the female abdomen is a potential synapomorphy for megalopygids and *Psycharium* (H. Geertsema, pers. comm.), although this trait also occurs in some zygaenids (Common, 1990).

Jordan (1909) noted the variation in shape and number of prongs (three or four) in the anal fork of presumably late instar *Somabrachys* collected at the same locality in Algeria. An early instar *Psycharium* sp. has five prongs, and late instar *Psycharium* have three and five prongs (from two USNM specimens of perhaps different species accidentally imported from unknown locations in South Africa (USNM)).

Minet (1986) considered the divided crochet mesoseries to be a symplesiomorphy between Somabrachyidae and the limacodid group. This condition, however, found in both *Psycharium* and *Somabrachys*, is not universally present in the Megalopygidae (Figures 253, 256) or Aididae (Figures 340, 343, 344). Although one group of the divided series may have been lost in some megalopygids and in dalcerids and crochet-bearing limacodids, it is also possible that the ancestral condition was undivided, as occurs in aidids or zygaenids.

Larval characters shared between the Somabrachyidae and Aididae do not provide support for common ancestry (see Aididae section, above). Prolegs without membranous pads, and the absence of spiracular sensilla in both families, appear to be plesiomorphic. The absence of crochets on A2 and A7 occurs frequently within megalopygids and dalcerids, as well. One potential synapomorphy would occur if the "missing" forewing radial vein in Somabrachyidae resulted from fusion between R_1 and R_2, because the two are stalked in Aididae. Jordan (1916:355) suggested that R_2 (= Sc^2) was absent. The loss, however, may have resulted from fusion of other stalked radial veins, including the most common in the limacodid group: R_3 and R_4 or R_4 and R_5.

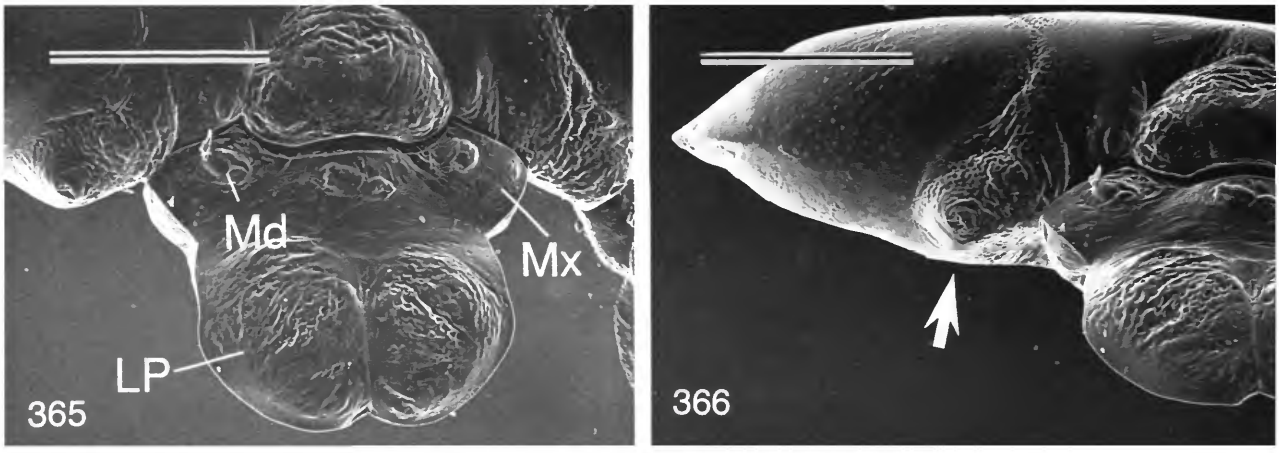
Based on the information presented, the best evidence for the membership of Somabrachyidae in the limacodid group is the presence of larval prolegs on A2 and A7. Somabrachyidae as the basal lineage of the limacodid group is suggested by putative plesiomorphies that are not found in the remaining families, including the large anal plate, anal comb, and relatively large thoracic legs in the larvae and the epiphysis in the adults (*Somabrachys*). Clearly, more information on *Somabrachys* and *Psycharium* is needed before the position of Somabrachyidae can be understood.

EPIPYROPIDAE Dyar, 1903, and CYCLOTORNIDAE Meyrick, 1912

DISCUSSION.—The cosmopolitan family Epipyropidae (Figure 42) has traditionally been difficult to place. This may be due to generalized wing venation, absence of mouthparts in the adults, highly reduced male genitalia, and hypermetamorphic larval stages with a penellipse of crochets. Adult characters have led to placement in or near Tineoidea (Forbes 1923; Turner, 1946; Brock, 1971); however, interpretations of larval and adult habitus have suggested placement in Zygaenoidea. The larval stages and biology of the Epipyropidae have been described and reviewed by Davis (1987) and Common (1990). The pupa was described by Heinrich (1931, pl. 2) and Common (1990).

The Australian family Cyclotornidae has many similarities with Epipyropidae, including hypermetamorphic and parasitic larvae (Davis, 1987; Common, 1990). The two families also share distinctive genitalic features. Females in both groups possess large secondary accessory glands that appear to perform a similar function. In dissecting a freshly killed female epipyropid, *Fulgoraecia exigua*, I observed that the large accessory gland was filled with a black fluid. Ovulated eggs in the common oviduct were white, whereas the eggs that had been laid were coated with the black secretion. A similar black fluid was reported in the Cyclotornidae (Common, 1990). Male genitalia in both families have reduced valvae and a paired gnathos (Common, 1990).

One difference between the Epipyropidae and Cyclotornidae is the crochet arrangement on the larval prolegs. In epipyropids the crochets on A3–A6 form a penellipse, whereas in cyclotornids they are in a mesoseries (Common, 1990). Indeed, the penellipse may be considered a plesiomorphic condition because it is found in lower ditrysian superfamilies; however, unless epipyropids are at the base of the Zygaenoidea, I suggest this to be a convergent condition. This is supported by the



FIGURES 365, 366.—Pupal head of Epipyropidae (*Fulgoraecia exigua*) (scale length in parentheses): 365, frontal view of labial palpi (200 μm); 366, frontoventral view, arrow points to lobe beneath eye (200 μm). (LP = labial palpus, Md = mandible, Mx = maxilla.)

presence of "retainer spines" on the crochets, which along with the penellipse appear to be a specialization for attachment to homopteran hosts (Davis, 1987).

Common (1990) reported another difference between epipyropids and cyclotornids: the spiracles on A1 of the pupa are hidden in *Heteropsyche* (Epipyropidae) but are visible in cyclotornids and in other Zygaenoidea. In the North American epipyropid species, *Fulgoraecia exigua,* however, the first abdominal spiracle is indeed visible. This character thus appears to vary within the family, much the way a visible second spiracle does in the Zygaenidae (Common, 1990).

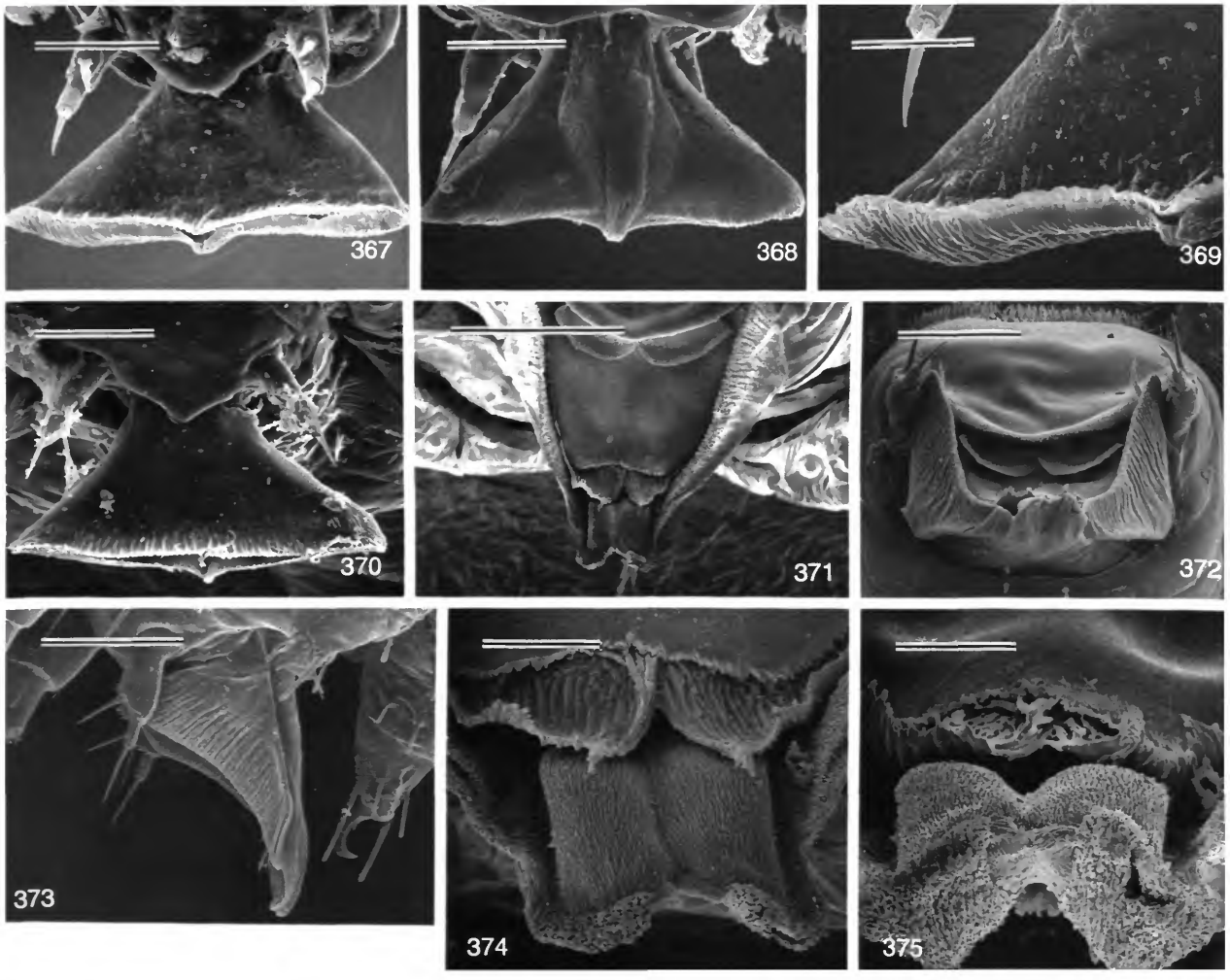
The pupal eyepiece in epipyropids (e.g., *F. exigua*) appears to lack the sculptured flange, which is synapomorphic for the limacodid group. A sculptured lobe (Figure 366), however, more mesal and below the eye, may be a homologous vestige. Another small lobe, contiguous with the labial palpus but lateral to it, may be a vestige of the maxilla (Figure 365). This would contradict Common (1990), who reported absence of the pupal maxilla in the Epipyropidae.

It is unlikely that Epipyropidae is the sister group to Dalceridae as suggested by Jordan (1928). Most of the characters shared between the two families are plesiomorphic; furthermore, a number of larval synapomorphies for Dalceridae + Limacodidae do not occur in Epipyropidae (Table 6).

Potential synapomorphies between the Epipyropidae and Cyclotornidae, including their parasitic habits, eggs, and female accessory glands, suggest that they form a monophyletic group. The pupal spiracle and female glands of epipyropids and cyclotornids are potential synapomorphies with other Zygaenoidea. A problem for future work will be determining the phylogenetic position of the two families within the superfamily. The absence of prolegs and crochets on A2 and A7 suggest placement outside of the limacodid group; however, more precise relationships are difficult to establish due to the specialized characters of parasitic larvae and to poor knowledge of subfamily relationships in Zygaenidae.

Ontogeny and Function of Limacodid Spinnerets

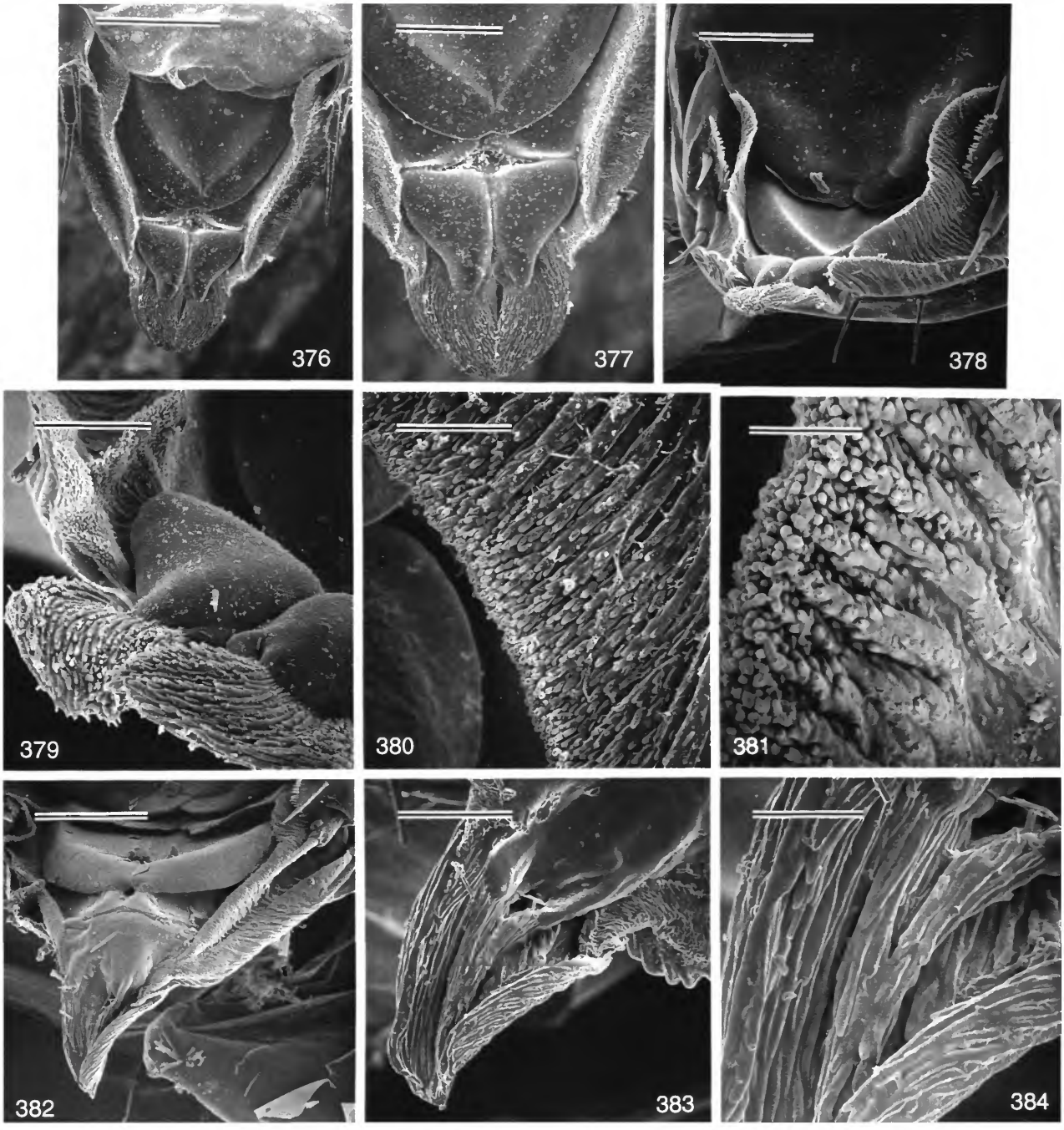
In this section, I describe the ontogeny and morphology of the spinneret in several limacodid species and discuss its homology and function. The spinneret of the *Semyra coarctata* complex, as in many limacodids, undergoes major ontogenetic change (Figures 367–384). First and second instars exhibit the common "fishtail" form (Figures 367–370). In the third instar, spinneret shape changes, with the base becoming wider than the tip. The upper lip, emarginate in the middle, is now shorter than the lower lip (Figure 371), and the lower lip has a spongy appearance (Figures 374, 375). The lateral portion, with numerous fissures leading from the dorsal margin, forms a soft flange (Figure 371–373). At the base of the spinneret are two elliptical lobes (Figures 371, 372). In the fourth instar, the most obvious change in the spinneret concerns the apex; the upper lip is subdivided into paired, smooth triangulate lobes with brush-like tips (Figures 376–379). The dorsum of the lower lip also is brush-like (Figure 379), and the lateral flange appears to be more spongy (Figures 380, 381). In the ultimate instar, the apex has a rag-mop appearance (Figures 382–384). Other



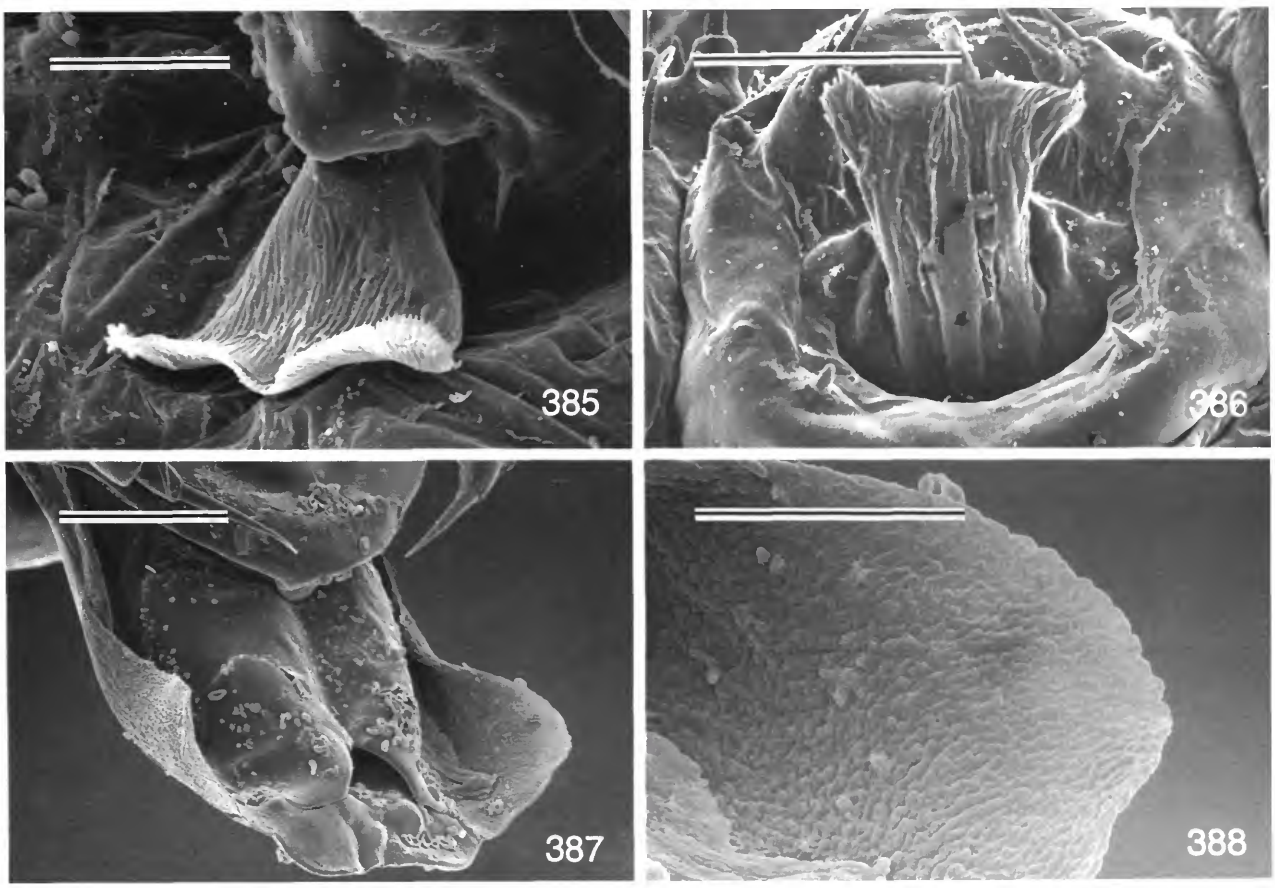
FIGURES 367–375.—Larval spinneret ontogeny of 1st through 3rd instar *Semyra coarctata* complex (Limacodidae) (scale length in parentheses). 367–369, 1st instar: 367, dorsum (20 μm); 368, ventrum (20 μm); 369, detail of dorsum (10 μm). 370, 2nd instar, dorsum (30 μm). 371–375, 3rd instar: 371, dorsum (100 μm); 372, frontoventral view (75 μm); 373, lateroventral view (100 μm); 374, detail of upper and lower lips of apex, dorsal view (20 μm); 375, detail of dorsal and ventral surfaces of apex, and silk pore (15 μm).

species exhibit a less dramatic ontogenetic change (e.g., *Talima postica*) (Figures 385–388).

The plesiomorphic state for the limacodid spinneret is to be apically wide. Often this condition is present only in early instars, as described above. First instars of a few species have parallel-sided spinnerets (e.g., *Crothaema, Phobetron, Apoda*) (Figures 389–392), similar to the condition found in megalopygids and many other lepidopteran larvae (Figures 142–147). Because of this similarity, parallel-sided spinnerets may seem to be the primitive condition for Limacodidae; however, the presence of apically-wide spinnerets in closely related genera of limacodids and in dalcerids suggests that the parallel-sided spinneret is derived. This is further supported by the presence of a rugose portion anterior to the opening, a condition that occurs in the wide spinneret of first instar *Pantoctaenia* (Figures 158, 159) but not in megalopygids or



FIGURES 376–384.—Larval spinneret ontogeny of 4th and ultimate *Semyra coarctata* complex (Limacodidae) (scale length in parentheses). 376–381, 4th instar: 376, dorsum (100 μm); 377, detail of dorsum (50 μm); 378, frontolateral view (75 μm); 379, detail of apex (20 μm); 380, detail of dorsal margin of lateral flange (10 μm); 381, detail of lateral flange (6 μm). 382–384, ultimate instar, from exuvia: 382, dorsum (75 μm); 383, apex (27 μm); 384, detail of apex (12 μm).



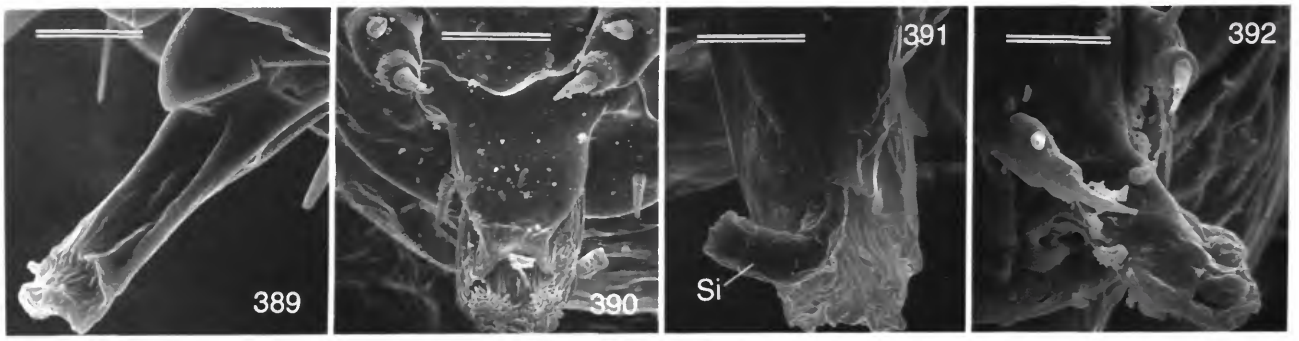
FIGURES 385-388.—Ontogeny of larval spinneret of *Talima postica* (Limacodidae) (scale length in parentheses). 385, 386, early instar: 385, dorsum (20 μm); 386, ventrum (20 μm). 387, 388, ultimate instar, from exuvia: 387, dorsum (50 μm); 388, detail of anterolateral margin (20 μm).

zygaenids. By the later instars, the shape of the once parallel-sided spinneret in *Phobetron* becomes more triangulate, much as in *Semyra*.

The diversity of spinneret form and function has been documented in several families of Lepidoptera. Ripley (1923) noted the correlation between brush-like spinnerets and the production of subterranean pupal cells in noctuids. MacKay (1963, 1964) reviewed possible relationships between spinneret form and function in Tortricidae and other Lepidoptera. Ontogenetic change in the spinnerets in limacodids was noted by Chapman (1893) and in notodontids by Miller (1991).

MacKay (1964) proposed that variation in silk-pore shape and the presence of apical fringes in noctuids (Ripley, 1923) must produce variation in silk shape and viscosity and in resulting silk function. Ripley (1923) interpreted "a very thin ribbon" of silk in limacodids (Chapman, 1894:347) to indicate that silk is issued in different physical states. The "narrowing" of the spinneret apex in middle-instar limacodids suggests the issuing of a more thread-like silk; however, this does not appear to be the case. Some of the cocoon silk applied by the narrowed spinneret in *Semyra* is ribbon-like (Figure 25). Furthermore, the apex of dalcerid spinnerets remains wider than the base in all instars, yet the larvae spin ribbon-like silk in first instars (Figure 156) and cover the outer portion of their cocoon with thread-like silk (Figures 18, 19).

The assumption that the size of the silk pore or the shape of the spinneret's anterior margin solely determines the type of silk ignores other potentially important aspects. In later instars of *Semyra*, the brush-like lateral margins may change the form of the silk during application to the substrate. Spinneret shape may also relate to non-silk functions, such as brushing off debris on the ventral surface of the thorax and abdomen, and the



FIGURES 389–392.—Parallel-sided larval spinnerets in 1st instar Limacodidae (dorsal view) (scale length in parentheses): 389, *Crothaema* sp. (6 μm). 390, 391, *Phobetron hipparchia:* 390, overall view, without silk (10 μm); 391, detail of tip and silk pore, with thread-like silk (6 μm). 392, *Apoda biguttata* (7.5 μm). (Si = silk.)

spreading of liquid Malpighian tubule secretions during cocoon construction (see "Biology," above).

Homology and Evolution of Larval Body Setae

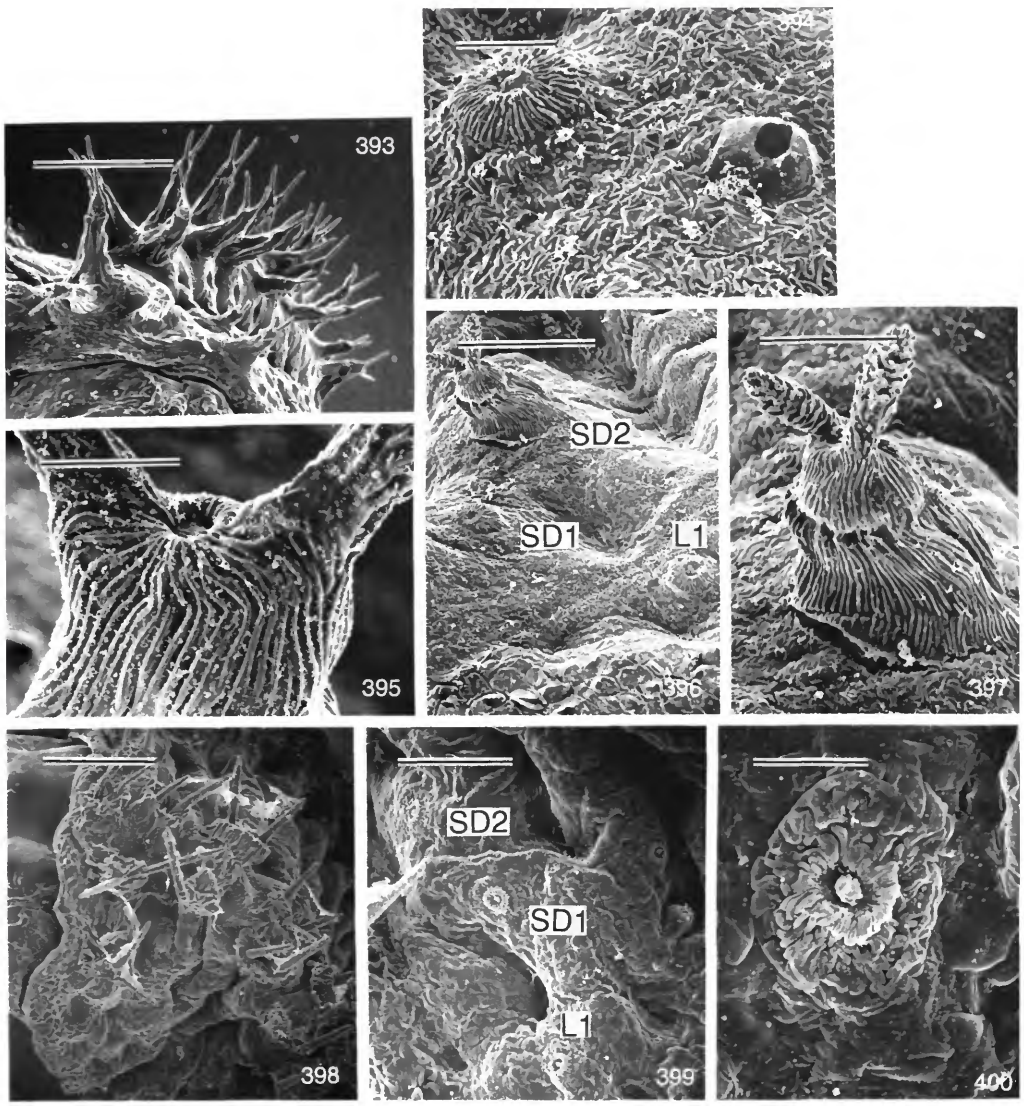
DALCERIDAE.—Setae on the dorsum of T2 and T3 and on segments A1–A9 in dalcerid caterpillars are covered with a gelatinous material, giving them a wart-like shape. Removal of this material reveals setae similar to primary setae found in most families of Lepidoptera (Figure 177). First instars in nonspiny lineages of Limacodidae have similar setal configurations (Figures 178, 179) but commonly have some degree of fusion or secondary branching (Figures 393, 395, 397).

There has not been a definitive homology for the body setae in dalcerids. The gelatin-covered setae have been incorrectly interpreted as smooth homologues of the spiny verrucae found in megalopygids, zygaenids, and many limacodids. Most abdominal segments in megalopygids and zygaenids have two verrucae, the D and SD, above the spiracles, and two below, the L and SV. Hopp (1928:285) mistakenly homologized the two D setae in dalcerids with D and SD verrucae, and the SD1 setae with L verrucae. The true L abdominal row in dalcerids consists of tactile setae proximate to the spiracles (Figures 180, 208, 209). Verrucae on T2 and T3 of megalopygids roughly match dalcerid setae in number and position, differing in the presence of only one SD group on T2 and T3 and one D group on T3. Stehr and McFarland (1987) considered the gelatinous setae in dalcerids to be secondary.

Dyar's (1925) homology concept for dalcerid setae is somewhat unclear. His setal terminology for *Acraga coa* is similar to that used in earlier work on the Limacodidae. According to Dyar (1925:45), the two D rows on segments A2–A6 are "subdorsal" and "lateral," corresponding to the two rows of verrucae or scoli dorsal to the spiracles in spiny limacodids. The third "suprastigmatal" row was probably viewed as an extra row. Dyar regarded the presence of only two rows, as found in megalopygids and zygaenids, to be the ancestral condition. In keeping with earlier larval descriptions, Dyar did not attempt to serially homologize dalcerid setae on the thorax with those on the abdomen (see next section).

LIMACODIDAE.—Limacodids are typically characterized as having either spined or smooth caterpillars. Early instars of smooth taxa often have long tubercles or Y-shaped setae in the D and SD positions (Figures 393, 397); however, *Belippa* (Figure 171), *Crothaema* (Figure 175), and *Pantoctaenia* (Figure 176) all have short cuticular warts. These warts occur in similar positions and bear a superficial resemblance to the gelatinous warts that cover dalcerid setae. *Olona* spp. are the only known limacodid larvae with gelatinous, dalcerid-like warts in late instars (Holloway, et al., 1987). This genus clearly belongs in the Limacodidae based on male genitalia and on the cocoon. Although I have not examined larval specimens of *Olona,* it appears from figures in Holloway et al. (1987) and in Piepers and Snellen (1900) that the larval warts are homologous with those found in dalcerids. I suspect that the L row of Holloway et al. (1987) is in fact an SD row as in the dalcerids. Holloway et al. (1987) noted that the warts do not correspond to the scoli of limacodids.

Other first instar limacodids have setal arrangements similar to dalcerids and the limacodid genera mentioned in the previous paragraph, although there is often some degree of fusion. Examples include the *Apoda, Phobetron,* and *Prolimacodes* complexes (Table 3). Dyar (1896a:179) considered the "Y-shaped setae" (= bisetose tubercles) found in first instar *Apoda* to be derived from the fusion of D1 and D2 (= Dyar's ia and ib) and SD1 and SD2 (= iia and iib). This hypothesis is supported by the presence of unfused pairs of D and SD setae on T2 and T3 (Figure 178) in the *Apoda* complex. Caterpillars of some species in this group (e.g., *Apoda biguttata*) have one arm of the Y shortened, producing nearly a simple tubercle



FIGURES 393–400.—Larval tubercles of 1st instar *Semyra* and *Prolimacodes* (Limacodidae) (scale length in parentheses). 393–397, *Semyra coarctata* complex: 393, anterolateral aspect (200 μm); 394, SD button and spiracle on A4 (10 μm); 395, detail of SD tubercle on T2 (10 μm); 396, SD and L tubercles and buttons on T3 (50 μm); 397, detail of SD2 tubercle on T3 (20 μm). 398–400, *Prolimacodes badia:* 398, anterolateral aspect (tubercles only partially everted) (86 μm); 399, SD and L buttons on T3 (compare SD2 with 396) (38 μm); 400, detail of SD2 button (8.6 μm). (L, SD = lateral-, subdorsal-group tubercles or buttons.)

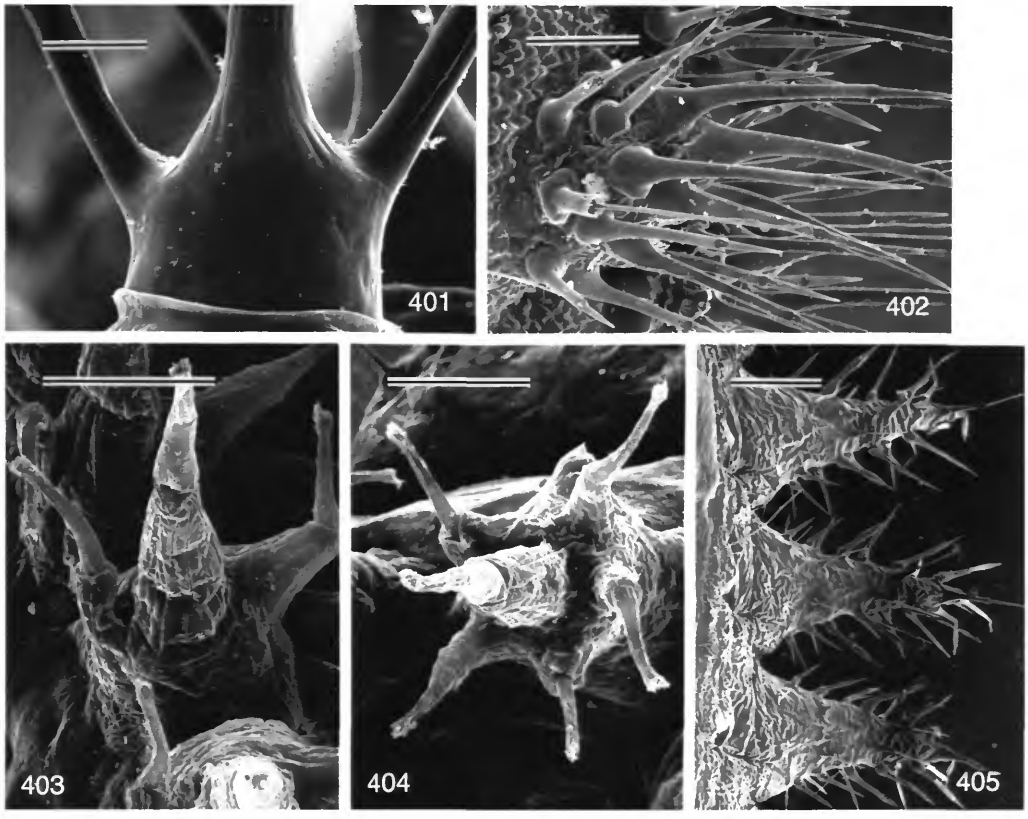
(Figure 195). This type of fusion and reduction was considered by Dyar (1896a) to explain evolution of tubercle shape in *Phobetron*.

Serial homology problems are inherent in Dyar's system for body setae. Dyar (1895a) considered the L (= iii) and SV (= iv and v) rows on the thorax to be homologous with the SD and L rows, respectively, on the abdomen. Dyar (1901) acknowledged this mistake in a reply to criticism from O. Hofmann (1898), but he chose not to make the necessary changes in deference to his earlier work. An example of this problem can be found in Dyar, 1896a. He reported that one of two pairs of D bisetose tubercles on the abdomen in first instar *Prolimacodes* (Limacodidae) represented the SD group (= Dyar's lateral row), moved dorsad of its normal position. This explanation, however, does not consider serial homology with thoracic setae. There is a pair of bisetose D tubercles in the

same position on T2 and T3 (see Figure 179, for closely related *Semyra*). Scanning electron microscopy in *Semyra* reveals an additional setal row, reduced to buttons near the spiracles (Figure 394). These setae, perhaps not visible to Dyar, likely represent the SD group. Reduction from tubercles to buttons can be seen when comparing the SD2 tubercle on T3 in *Semyra* (Figures 396, 397) and *Prolimacodes* (Figures 399, 400).

First instar spiny limacodids have at least three setae per tubercle (Figures 401, 403; see also Figures 172, 174), whereas later instars have a maximum of four scoli per segment, (two on each side) (Dyar, 1899a). In the *Natada* complex (e.g., *Euprosterna*), first instars have the three setae on the abdominal tubercles (Figure 403), but there are seven on the thoracic tubercles (Figure 404) (see also Dyar, 1899d, pl. 1). Some of these setae are likely to be secondary, but others may have evolved by fusion of tubercles. For example, three setae on a D tubercle may result from fusion of two bisetose D tubercles as found in the *Semyra coarctata* complex (Figures 179, 393). In contrast to the variable number of setae in the *Natada* complex, first instars of the spiny *Parasa* complex have three setae on every tubercle. These also differ in being more fused at the base and by having sharper points (Figures 174, 206, 401).

EVOLUTION AND ORIGIN.—The sister-group relationship between limacodids and dalcerids sheds light on the evolution of scoli in the Limacodidae. The presence of primary setae in positions homologous to those found in dalcerids is plesiomorphic in the Limacodidae (Figures 180, 181). Often only occurring in the first instar, these setae are in the form of warts or tubercles. I suspect that the common ancestor of the Limacodidae and Dalceridae had thick, unfused primary setae or tubercles, similar to the setae beneath the gelatinous secretions in the Dalceridae (Figure 327). Limacodids with primitive body setae in first instars include *Pantoctaenia, Crothaema,* and *Belippa.* Body setae in the *Semyra* and *Apoda* complexes also are primitive but have some degree of fusion (Figures 178, 179). No taxa with scoli in late instars have been found to have the primitive setal arrangement. This



FIGURES 401–405.—First and 3rd instar scoli of spiny Limacodidae (scale length in parentheses). 401–402, *Talima postica:* 401, trisetose scolus of thorax, 1st instar (10 μm); 402, SD scolus on mesothorax, 2nd or 3rd instar (50 μm). 403–404, *Euprosterna* sp., 1st instar: 403, D scolus on abdomen (50 μm); 404, thoracic scolus (50 μm). 405, *Natada subpectinata,* middle instar, SD abdominal scoli (200 μm).

contradicts the hypothesis that the limacodid ancestor was spiny, based on a phylogeny with a megalopygid- or zygaenid-like ancestor (Dyar, 1899a; Holloway, 1986).

The evolution of cuticular warts from thick primary setae can be hypothesized in the following manner. Warts in first instar limacodids (e.g., in *Crothaema* and *Pantoctaenia*) may represent tubercles that have remained enclosed in their bases and have fused in the embryo, rather than telescoping outward upon hatching. "Buttons" found on warts of other primitive limacodids may represent the distal end of tubercles that extended just beyond the base, with the remainder undergoing fusion and reduction in the embryo (e.g., *Belippa,* Figures 188–190). This is plausible because buttons are quite similar to the tips of normal tubercles (Figure 395), and they occur in homologous positions to the tubercles of related taxa that evert after eclosion (compare SD2 button in *Prolimacodes* and bisetose SD2 tubercle in *Semyra;* Figures 396, 397, 399, 400). Partial fusion may explain the condition of SD tubercles in first instar *Heuretes* and *Alarodia* (Figures 199, 200), which are short in relation to the D and SD tubercles found in related *Phobetron* spp. of the same stage (Figure 203).

Everted tubercles and warts in the limacodid embryo may relate to the evolution of a flat, scale-like egg with a thin chorion. Spiny verrucae, found in first instar megalopygids, are possibly correlated with a thicker chorion because urticating setae could more easily damage a thin chorion.

L or SV verrucae in zygaenids, megalopygids, and somabrachyids serve a defensive function. The presence of primary setae and the reduction of verrucae in the L and SV positions in the aidid + (limacodid + dalcerid) clade appear related to a more slug-like locomotion and to the greater contact of the lateral and ventral surfaces with the substrate that results. The link between setal reduction and locomotion can be seen in the following two examples. When comparing the ontogeny of L and SV setae in *Zygaena trifolii* during the first three instars, L setae increase with each instar, whereas the three SV setae on the proleg planta are unchanged (Tremewan, 1985). Clearly, SV setae have more direct contact with the substrate than L setae during locomotion. Dalcerids and spiny limacodids show a similar trend when one compares the type of L setae between the thorax and abdomen (Figures 177–181). In contact with the substrate, the L setae on the abdomen are hair-like or fungiform, whereas those on T2 and T3, farther removed from the substrate, are defensive, gelatin-covered setae or scoli.

It has been suggested that the two L setae in limacodids evolved by reduction of L verrucae as found in megalopygids (Figure 406) and zygaenids (Dyar and Morton, 1895). I propose that L setae in aidids (Figure 407) represent an intermediate condition between L setae found in megalopygids and limacodids + dalcerids, in which the setae-bearing warts found in megalopygids are formed but do not develop dense secondary setae. In the limacodid + dalcerid clade these warts are lost (or retained, e.g. *Crothaema*), whereas the primary setae remain (see further discussion in "Homology of Suckers," below).

Evolution of the Ventral Abdominal Surface

Dyar (1894:212) and Stehr and McFarland (1985) considered the presence of prolegs on A2 and A7 to be derived from an ancestral condition of prolegs on A3–A6 (Hinton, 1955; Common, 1975). Dyar's contemporaries had several other interpretations. Packard (1894) suggested that prolegs on A2 and A7 represent a persistent, ancient condition within Lepidoptera. Chapman (1893:115) considered the "apod character" of the ventral surface in limacodids to be the result of "very recent descent from a footless mining larva," although he later wrote that limacodid suckers were "homologous with prolegs, and also with the eight pairs of abdominal legs of *Eriocephala* [= Micropterygidae]" (Chapman, 1894:345). Dyar (1895a, 1899b) considered limacodid "suckerdisks" to be derived from the medial fusion of pads on megalopygid prolegs. He further believed that suckers on A1 and A8 were not derived from prolegs, but he did not suggest their origin (Dyar, 1899b).

PROLEGS AND CROCHETS.—A new interpretation of how the ventral abdominal surface evolved on proleg-bearing segments in the limacodid group, based on my phylogenetic evidence, is as follows: (1) the limacodid-group ancestor gained additional crochet-bearing prolegs on A2 and A7; (2) in the aidid ancestor, dense plumose SV setae on proleg bases, as found in megalopygids, were lost; (3) the limacodid + dalcerid ancestor had reduction of proleg size, suckers formed from lateral proleg bases on A2–A7, and crochets were not phenotypically expressed until after the first instar (on A2–A7 and A10); (4) post-first instar crochets were lost on A10 and at least once on A2 and A7 in Dalceridae; and (5) post-first instar crochets were lost in all lineages of Limacodidae examined except *Pantoctaenia* (present on A2–A7 and A10).

According to this hypothesis, crochets were present on A2 and A7 in ancestors of both megalopygids and dalcerids and were independently lost in each lineage. An equal size and number of crochets on each crochet-bearing segment in *Pantoctaenia* may represent the ancestral condition for the Limacodidae + Dalceridae clade. The smaller and less numerous crochets on A2 and A7 in *Dalcerides ingenita* (Stehr and McFarland, 1985, 1987) may represent the stage prior to their complete loss on these segments in other dalcerids. Intermediate stages of crochet loss between the condition found in *Pantoctaenia* and the condition in other limacodids have not been observed. Crochets are absent on A2 and A7 in all Aididae and Somabrachyidae so far examined. A sister-group relationship of either family to megalopygids or of aidids to limacodids + dalcerids suggests that the crochets were present in the common ancestor.

The discovery of crochets on A2 and A7 in the Dalceridae by Stehr and McFarland (1985) provided new evidence of their relationship with the Megalopygidae. Previous to this finding, megalopygids had been the only family of Lepidoptera reported to have prolegs on these two segments. They proposed an evolutionary progression for proleg development in the

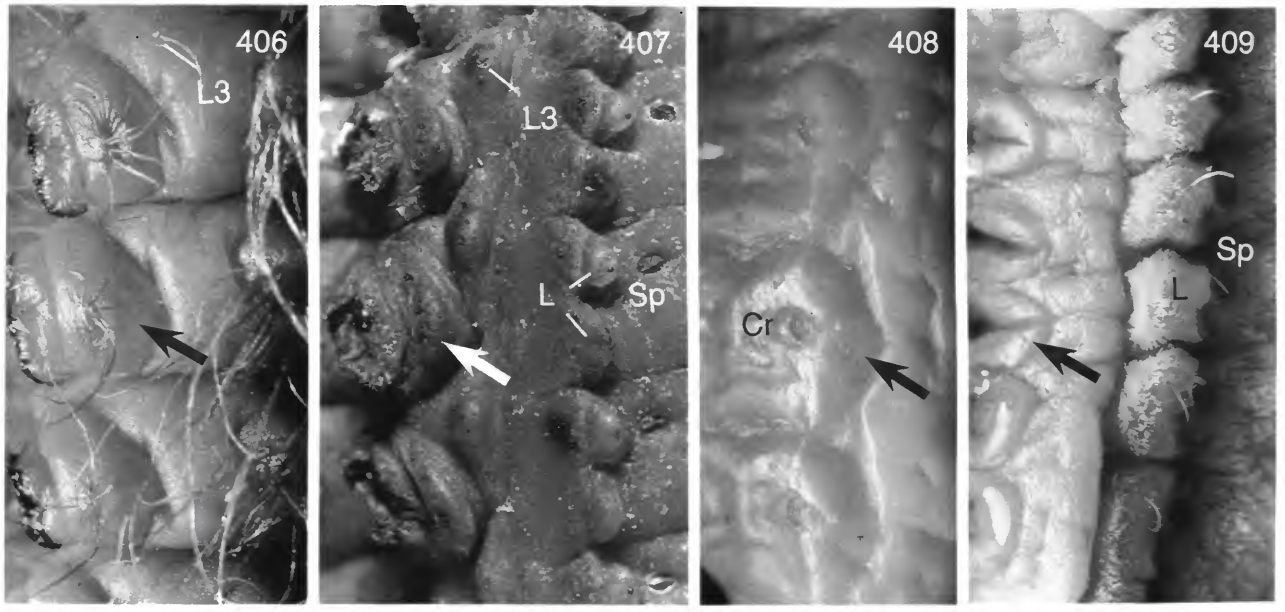
Zygaenoidea that went from "an ancestor with equal-sized prolegs with crochets on A2–A7, to the dalcerids with smaller prolegs and reduced numbers of crochets on A2 and A7, to the megalopygids with smaller prolegs and no crochets on A2 and A7, to the limacodids with all prolegs reduced to suckers and crochets totally absent" (Stehr and McFarland, 1987:461).

My phylogenetic analysis (Figure 326), which includes both characters of immature stages and of adults, clearly rules out Dalceridae as ancestral to Limacodidae + Megalopygidae; however, this also is true if one exclusively examines prolegs and crochets. The discovery of megalopygid larvae with prolegs of equal size and with equal numbers of crochets on A2–A7 (Figures 216, 252, 253) eliminates the need to evoke a hypothetical ancestor with this condition. Furthermore, the presence of crochets on A2–A7 and on A10 in *Pantoctaenia* (Figures 358–360) suggests this as the ground-plan state for limacodids. A similar degree of sucker development in primitive limacodids (Figures 219, 266) and in dalcerids (Figures 261) supports the occurrence of suckers in the ancestor of Limacodidae + Dalceridae (see further discussion in "Homology of Suckers" below).

I have interpreted the presence of crochets on A2 and A7 as a synapomorphy for the limacodid group, although they are more frequently absent than present in megalopygids and dalcerids. Crochets on A2 and A7 have not been found thus far in aidids or somabrachyids. Perhaps the presence or absence of crochets on these segments is controlled by a gene that switches expression on or off. If this were the case, it raises the question whether prolegs and crochets on A2 and A7 are suppressed in other groups of Lepidoptera.

The presence or absence of crochets in dalcerids and limacodids can be viewed in terms of developmental timing, or heterochrony. The delay of crochet development until after the first instar in dalcerids (Figures 262, 263) and in *Pantoctaenia* (Figures 360, 361), and subsequent addition of crochets on A2 and A7 in *Dalcerides ingenita*, are examples of postdisplacement, a late start in development (Funk and Brooks, 1990). In the context of heterochrony, the absence of crochets in known limacodids other than *Pantoctaenia* may have resulted from progenesis, an early stop in their development (Funk and Brooks, 1990). Studies on the genetics of crochet expression should be pursued in future molecular or developmental research.

HOMOLOGY OF SUCKERS.—The lateral portion of the proleg base on A2–A7, which bears SV verrucae in the Megalopygidae, appears to be homologous with the suckers in the limacodid + dalcerid clade. This is best seen when comparing proleg bases, along with L and SV setal rows, in representative megalopygids, aidids, dalcerids, and limacodids (Figures 406–409). The proleg base is laterally convex in megalopygids and aidids (Figures 406, 407). Aidids have an intermediate condition in which the dense setae are lost. Through further



FIGURES 406–409.—Evolutionary hypothesis of proleg reduction and the formation of suckers in the limacodid group (arrows point to lateral margin of proleg base and to lateral margin of suckers) (406, 408 photos by C. Hansen; 407, 409 photos by L. Minor-Penland): 406, *Megalopyge lanata* (Megalopyginae); 407, *Aidos* sp. (Aididae); 408, *Dalcerina tijucana* (Dalceridae); 409, *Acharia* sp. (Limacodidae). (Sp = spiracle, Cr = crochets, L = lateral-group setae.)

reduction, the proleg base forms the lateral portion of the suckers in dalcerids and limacodids (Figures 408, 409).

Suckers may have been derived on nonproleg-bearing segments in the following manner. In megalopygids, A1 and A8 each have two SV verrucae, one lateral to the other, whereas A9 has only one, in line with the more mesal member of A8. Aidids have presumably homologous warts, although these do not bear long secondary setae. It is these verrucae or warts, rather than prolegs, on A1 and A8 that likely form the lateral margins of the suckers. Suckers on these two segments, often poorly developed or absent, are well developed in late stage *Pantoctaenia* (Figures 219, 358).

The longitudinal ridge and bordering depression mesad between the two L warts and the proleg bases in aidids (Figure 339) may be the precursor of the subspiracular flange in Limacodidae described by Holloway (1986). The region of flexible cuticle, below the flange and lateral to the suckers in limacodids and dalcerids, may have been derived in part from the L3 verrucae or warts in megalopygids and aidids. The presence of the L3 wart in the Aididae, without plumose setae, is a plausible intermediate stage (Figure 407).

My evolutionary hypothesis of the ventral surface in limacodids differs from previous interpretations. According to Dyar (1895a, 1899b), limacodid suckers are derived from an extension of the membranous pads found on megalopygid prolegs. This is not supported, because membranous pads appear to be uniquely derived in megalopygids and absent in aidids, the group considered herein to be ancestral to limacodids and dalcerids. Moreover, the lateral portions of prolegs more closely resemble the lateral margins of the suckers. The pads would have had to become greatly expanded to achieve this configuration.

Character states in dalcerids and *Pantoctaenia* suggest that both suckers and crochets were present in the limacodid + dalcerid ancestor. Previous interpretations proposed that crochets were lost prior to (Holloway, 1986:52) or after the formation of suckers in the limacodid ancestor (Dyar, 1899b).

FUNCTION AND ADAPTATION.—I hypothesize that extra prolegs and a slug-like ventral surface benefit larvae, whether at rest or in motion, by increasing adhesion to the substrate. In families with discernable prolegs (e.g., megalopygids and aidids), additional prolegs and the shortened ventral segments on A8–A9 provide a broader adhesive zone on flat leaf surfaces than is normally found in external-feeding caterpillars (Figures 215–218, 223). Extra prolegs may also increase the clasping ability of a larva lengthwise on a leaf edge or stem. In spite of reductions in proleg size and crochets, limacodid and dalcerid larvae are adept at medially clasping narrow surfaces due to the retention of ventral muscles and the flexibility of the ventral surface.

Further, I suggest that the ventral surface and brush-like spinneret of the caterpillars in the limacodid + dalcerid clade represent apomorphic function (sensu Coddington, 1988) and are an adaptation for existence on smooth leaf surfaces. Dyar (1899a:241) observed that temperate limacodids "principally frequent smooth, glabrous leaves of trees and shrubs." The flexible and sticky ventral surface in the clade provides maximum contact with the substrate. The function of this type of ventrum can be seen when comparing the crawling abilities of limacodids and dalcerids to that of megalopygids. The slug-like larvae of the first two families have little problem crawling on glass at any slope, including upside down, whereas megalopygids easily become dislodged and can only make an attempt to stay on the glass by spinning copious amounts of silk. Limacodid and dalcerid larvae also have the advantage of having a ventral surface that is sticky and in continuous motion. They do not have to plant each segment individually as do larvae with prolegs. The presence of suckers in limacodid and dalcerid larvae may also contribute to this ability.

Larvae in the limacodid group feed on either leaf surface. In megalopygids and aidids, the ability to feed while clinging underneath leaf surfaces is presumably enhanced by the large numbers of crochets and the spinning of large quantities of silk but not necessarily by their extra prolegs, which commonly lack crochets. Dalcerid caterpillars (e.g., *Dalcerides ingenita*) are difficult to detect while they are feeding on leaf undersurfaces (Stehr and McFarland, 1985). Limacodid caterpillars may feed on either leaf surface (e.g., *Phobetron pithecium*) (Dyar, 1896a:180) or may feed soley on undersurfaces (e.g., *Isa textula* (Herrich-Schäffer) (Dyar, 1896a:187).

The presence of membranous pads in megalopygids may help the larvae adhere to smooth surfaces. In conjunction with prolegs, the pads can stick to glass while the crochets are turned under (pers. obs.; Dyar, 1899b). Dyar (1899b) considered this to be an adaptation for allowing polyphagous larvae to feed or crawl on smooth or rough surfaces. Retractor muscles are likely attached to these pads as evidenced by the presence of dense muscle tissue attached to the ventral surface of megalopygid larvae. This may produce a degree of suction, such as described for plantae by Hinton (1955). Further elaboration involves the modification of SV verrucae into an additional row of membranous pads in *Mesocia pusilla* (Figure 252). The absence of crochets on A2 and A7 in the majority of megalopygid and aidid larvae, presumably independent losses, may have similar function to the pads.

It appears that *Psycharium* larvae, which lack the membranous pads (Figures 217, 249), are specialized for clinging to narrow leaf surfaces found on their narrow-leaf hosts, such as Restionaceae and *Pinus* (H. Geertsema, pers comm.). When placed on a smooth glass surface, early instar *Psycharium* larvae clasp prolegs together rather than place them on the substrate (pers. obs.).

There have been other suggestions regarding the adaptive significance of the slug-like ventral surface. Packard (1890:148) stated that the "slow gliding motion" of smooth, nonspiny limacodid species "renders them less liable to be

observed by passing birds." There may indeed be some cryptic advantage in lacking prolegs, because typical caterpillars can be detected by their prolegs when crawling on leaf edges. The locomotion in smooth species, however, surely did not evolve independently from the more visible spiny limacodids as suggested by Packard's Neo-Lamarckian philosophy (Packard, 1895b:83–84).

The presence of larval crochets in a mesoseries may be considered a synapomorphy for the Zygaenoidea because potential sister groups in the lower Ditrysia have crochets in an ellipse. Hinton (1955:502–503) hypothesized that larvae with crochets in mesoseries are adapted for climbing. He based this on the ability of a larva with this arrangement of crochets to medially clasp twigs and on the appearance of this characteristic in "all exclusively arboreal caterpillars" that are external feeders. He suggested that this development evolved independently in higher (e.g., papilionids) and lower ditrysian groups (e.g., zygaenids). A test of whether the presence of mesoseries in the Zygaenoidea represents an adaptation (in a cladistic sense) for climbing has potentially been made because possible outgroups (e.g., cossoids, sesioids, tortricoids) are not tree climbers, and it is improbable that a mesoseries is plesiomorphic in the lower Ditrysia.

Future comparative studies on the energetics and biomechanics of locomotion in the limacodid group are warranted. One approach would be to measure the energetic cost of locomotion by measuring oxygen consumption (Denny, 1980; Casey, 1991). Perhaps the cost of additional prolegs in megalopygids could be estimated by comparing megalopygid oxygen consumption with that of external-feeding caterpillars having typical numbers of prolegs (e.g., gypsy moth larvae; Casey, 1991). It also would be worthwhile to determine if the cost of locomotion in limacodid and dalcerid caterpillars is similar to that of an analogue group, such as terrestrial slugs (Denny, 1980).

Summary

The phylogenetic analyses described herein, which include separate and combined data sets of both adult and immature stages, support a monophyletic Megalopygidae consisting of Megalopyginae + Trosiinae at the base of the limacodid group. Formerly a subfamily of Megalopygidae, Aididae is found to be the sister group of the Limacodidae + Dalceridae clade. It is clear that aidids do not form a clade with either megalopygid subfamily, and contrary to previous assertions, they do not belong within the Limacodidae. Chrysopolomidae is placed as a subfamily within Limacodidae, based on synapomorphies with apparently higher lineages of Limacodidae, but subfamilial status is provisional until a more detailed study of limacodid classification can be undertaken. Further work is needed on the Somabrachyidae to determine whether *Somabrachys* and *Psycharium* are sister genera or belong in Megalopygidae. They share a number of characters with megalopygids, but most can be argued to be symplesiomorphies in relation to the Megalopygidae or the Zygaenoidea.

Synapomorphies for the limacodid group include the presence of abdominal segments A2 and A7 with crochets, ventral reduction of segments A8 and A9, reduction of the anal plate, and short prolegs in the larva; short maxilla and sculptured flange on the eyepiece of the pupa; and absent ocelli, short galeae, and dense sensilla trichodea on the fifth tarsomere of females of the adult. The Limacodidae + Dalceridae clade is strongly supported by synapomorphies including fungiform SV and V setae, absence of crochets in early instars, highly reduced prolegs and thoracic legs, a brush-like spinneret, absence of S2 seta and anal fork, elongate axial seta, presence of frass-flipping setae, and smooth ventral surface in the larva and absence of chaetosemata, reduced sclerite on the mesepimeron, and presence of a gnathos in the adult.

A second phylogenetic analysis, using adult and immature stages, is also performed to diagnose the placement of African limacodid genera *Pantoctaenia* and *Crothaema*. Each genus is found to have a number of primitive character states in the immature stages, some shared with Dalceridae (e.g., crochets), but not found in other Limacodidae. The results are inconclusive, showing the genera to be either a primitive group of Limacodidae (combined and adult data) or the sister group to Limacodidae + Dalceridae (data of immatures). Congruent cladograms result with *Pantoctaenia* and *Crothaema* as primitive Limacodidae, however, by recoding two potentially weak characters of the A10 prolegs, one as convergent losses of crochets rather than as a synapomorphy, and the other as a loss of frass-flipping setae rather than as a plesiomorphy.

The presence of exposed abdominal spiracles in the pupa and the female secondary accessory glands in epipyropids and cyclotornids lends support for placing these groups in Zygaenoidea. A more distant relationship, however, between Epipyropidae and the limacodid group (especially Dalceridae) than previously thought is suggested based on a large number of synapomorphies between Dalceridae and Limacodidae and the presence of either crochets or prolegs on A2 and A7 in all limacodid-group families but not in epipyropids.

The phylogeny of the limacodid group suggests new interpretations of the evolution of the limacodid ventral surface. Prolegs in the Limacodidae are often reported as being absent or modified into suckers. It is proposed that suckers on A2–A7 are homologous with the lateral portion of the proleg bases, which bear SV verrucae in Megalopygidae, and it is proposed that suckers on A1 and A8 are derived from verrucae or warts, as found in megalopygids and aidids, and are not homologous with prolegs. Delayed appearance of larval crochets until the middle or late instars of dalcerid species and primitive limacodid species (e.g., *Pantoctaenia*) suggests that the absence of crochets in most limacodids evolved from an

early termination in their expression during the larval stage rather than during the embryonic stages.

The homology of several confusing character states in the limacodid group is clarified. Removal of the gelatinous warts on dalcerid larvae reveals primary setae that are homologous to those found in early instars of limacodids with smooth later instars, rather than homologous with verrucae found in zygaenids and megalopygids as has been previously implied. SV setae, unreported or considered absent in Limacodidae and Dalceridae, occur as modified fungiform setae on the slug-like ventrum. The "ventral valva" of the male genitalia in Megalopygidae is reinterpreted as a juxtal lobe, based on the condition of the juxta in Aididae and Dalceridae.

Behavioral observations of limacodid and dalcerid larvae show that semifluid silk is the liquid observed on the ventral surface, and brush-like spinnerets in the two families are used to remove debris from the ventrum. Spinnerets in the Limacodidae may undergo major changes in shape between instars, whereas spinneret shape in the Dalceridae remains unchanged.

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