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The external morphology of the egg and larval stages of Hemerobius stigma Stephens (Neuroptera: Hemerobiidae) with reference to life history and notes on a larval parasite

Gary L. Miller

To the Graduate Council:

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Paris L. Lambdin, Major Professor

We have read this thesis and recommend its acceptance:

Reid R. Gerhardt, M. L. Pan

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

THE EXTERNAL MORPHOLOGY OF THE EGG AND LARVAL STAGES OF *HEMEROBIUS STIGMA* STEPHENS (NEUROPTERA: HEMEROBIIDAE) WITH REFERENCE TO LIFE HISTORY AND NOTES ON A LARVAL PARASITE

A Thesis

Presented for the

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Gary L. Miller

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ABSTRACT

Identification of Hemerobius stigma Stephens is currently based only on adult morphological characters. This study provides additional morphological means to distinguish H. stigma from other hemerobiid species.

The three larval stages of H. stigma can be distinguished by the number of setae present on the posterior annulet of abdominal segment 10 and the presence or absence of a trumpet shaped empodium. Taxonomic keys to the larval stages are included as well as life tables with notes on larval and adult feeding habits, fecundity, ovipositional preference and egg morphology.

Ovipositional habits and life history data were recorded for Anacharus sp. (Figitidae), reared from parasitized H. stigma larvae.

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CHAPTER I

INTRODUCTION

One hundred years passed between Leach's (1815) establishment of the family Hemerobiidae and Moznette's (1915) presentation of the first account of a life history. By the time Carpenter (1940) revised the family, the life histories of only six of the 50 Nearctic species were known. The European species were more thoroughly investigated with the life histories completed for 18 of the 29 species listed in Killington's (1936, 1937) monograph of the British Neuroptera. Balduf (1939) summarized most of the earlier literature concerning the Hemerobiidae. More recently, New (1975) published a review of selected literature on the biology of Chrysopidae and Hemerobiidae. His work contained relatively few contributions relating to the life histories of hemerobiids since Balduf's (1939) work.

Early investigations into the life histories of the Nearctic Hemerobiidae were presented by Moznette (1915), Cutright (1923), and Smith (1923) while major life history studies of Palearctic Hemerobiidae were prepared by Withycombe (1923) and Killington (1937). I conducted this investigation to describe the egg morphology of H. stigma, to differentiate the larval stages by examining and describing chaetotaxy, and to compile life tables with notes on behavior. I also recorded observations on parasitic figitid (Anacharus sp.) wasps which emerged from some H. stigma larvae.

CHAPTER II

LITERATURE REVIEW

I. NEUROPTERA

The Neuroptera, commonly known as lacewings, nervewings, and netwings, constitute one of the smaller orders of Insecta. Austen (1931) estimated that Neuroptera contained 3,500 species worldwide. Sabrosky (1952) increased this estimate to include 4,670 species with 338 occurring in America north of Mexico. The vast majority of Neuroptera are predacious in either the larval stage or as both larva and adult. With the exception of Odonata, probably no other insect group is so completely predacious upon other insects (Balduf 1939).

Morphologically, neuropteran larvae are distinguished by enlarged grooved mandibles and maxillae that form a mandibular canal leading to the pharynx. Liquified food is drawn through the canal into the pharynx via pumping action of the pharyngeal region. There is no evidence of extraoral digestion (Carpenter 1940). The larval digestive tract is closed at the posterior end of the ventriculus resulting in the elimination of excreta in the form of a meconial pellet after reaching the adult stage.

Eggs of Neuroptera possess a micropylar knob (Balduf 1939) and the surface of the chorion of many neuropteran families is deeply set with projections. The projections serve to trap a film of air when eggs are flooded, protect the general surface against the effects of turbulence,

and establish a humidity gradient that retards water loss (Hinton 1981).

The neuropteran suborder, Planipennia, have three larval instars. These stages differ from each other in numerous ways other than size. Withycombe (1923) considered two important differences in the planipennian instars: (1) loss of the empodium of first instars upon molting into second or third instars and (2) the number of setae and their form. In chrysopid larvae, the tips of the setae of first instar larvae are hooked while second and third instar larvae have hooked setae only if that species habitually carries debris. Lateral warts on first instar chrysopids have two setae while subsequent instars exhibit a brush of setae on these warts. All first instar larvae have fewer body setae than in later stages and the chaetotaxy is very similar throughout the order (Withycombe 1923).

Planipennian larvae pass their pupal stage in silken cocoons. Fluid diffuses from modified Malpighian tubules into the silk reservoir, passing to the rectum and anus where silk is spun (Carpenter 1940). Upon emergence, the pharate adult cuts a hole in its cocoon with its mandibles. It exits the cocoon completely and finds a suitable substrate. Here the pupal exuvia is cast, and the process of tanning occurs. Adults are usually crepuscular or even nocturnal; their longevity may vary depending on the species.

II. HEMEROBIIDAE

The family Hemerobiidae was established by Leach in 1815. Hemerobiidae is derived from a Greek misnomer meaning living for a day.

As late as 1905, Banks believed the adults lived for a week or two. The adults of some species may live as long as five months (MacLeod and Stange 1981). These small to medium sized brown Neuroptera are strictly terrestrial and are predaceous as larvae and adults. Species of this taxon are commonly referred to as brown lacewings and aphid wolves. New (1975) reported 99 species referrable to Hemerobiidae with representatives in 12 regions, but failed to include the 60 species from the Nearctic region (Nakahara 1965). New (1975) believed indigenous species could be used as biocontrol agents. Within the order Neuroptera, Balduf (1939) considered Hemerobiidae second in importance to Chrysopidae as predators of small, soft-bodied insect pests. Hagen and van den Bosch (1968) implied that the Neuroptera had considerably less value in aphid control than some other groups of predators.

The process of feeding and cocoon spinning is similar to other Planipennia. Larvae are fusiform resembling those of chrysopids, but have no empodia in the second and third instars. Withycombe (1923) described the body as sparingly clothed with fine setae arranged in a constant pattern throughout all species of Hemerobius. Chaetotaxy, pigmentation, and arrangement of sclerites are useless characters for differentiating species of Hemerobius (Withycombe 1923). Unlike larvae of some species of Chrysopidae, hemerobiids do not carry debris on their dorsums. Although the misconception still persists that hemerobiid larvae carry debris (Comstock 1940; Milne and Milne 1980), no species is known to exhibit this behavior (Killington 1934). Hemerobiid larvae have a broadly rounded head with six ocelli, 3-segmented antennae with

second and third segments annulated and an apical seta on the third segment, mandibles with apical ridges and serrations, maxillae length and shape similar to mandibles but blunt at the apex, and 3-segmented labial palpi; thoracic segments membranous with reduced dorsal sclerites, cursorial legs; abdomen 10-segmented, dorsal sclerites reduced on first eight segments, ninth and tenth segments sclerotized, and an anal papillus that serves as a holdfast structure during molts (Killington 1936).

The Hemerobiidae undergo three larval instars with a molting process similar to that of the Chrysopidae (Smith 1923). After the third stage larva is fully fed, it enters a prepupal stage (the "pharate pupa" of Hinton 1963). A two part cocoon is spun from silk and the larva draws its legs close to the body while bending the head, prothorax and tip of abdomen ventrad (Killington 1936). The pupal stage is marked by development of long antennae, compound eyes and wing pads. Prior to adult emergence, the pupa cuts an emergence hole in the cocoon and sheds its exuvia. The newly emerged adult begins expansion movements and after tanning, eliminates a meconial pellet.

Adult hemerobiids are characterized by: moniliform antennae, well-developed compound eyes, but lack ocelli; prothorax broader than long, legs cursorial; wings subequal, held in roof-like position over abdomen, forewing with numerous crossveins and longitudinal veins branched toward inner and outer margins, hindwing with unbranched veinlets; abdomen 10-segmented, male tenth sternite modified to form an internal plate, females with reduced eighth sternite (Killington 1936; Carpenter 1940).

General descriptions of hemerobiid eggs were provided by Smith (1923), Withycombe (1923), Killington (1936, 1937), and Carpenter (1940). Hatching is essentially the same throughout the family and was described by Smith (1922).

The larval prey are relatively small with a cuticle that is easily penetrable. Since aphids, coccids, cicadellids, thrips and mites predominate as agricultural pests, the Hemerobiidae constitute an important biocontrol agent (Balduf 1939). This aspect combined with evidence that some hemerobiid species are tolerant to various insecticides (Reeve and French 1978) increases the potential use of this family in integrated control programs. Hemerobius pacificus Banks is able to reproduce in the winter and has extremely low temperature thresholds for the immature stages (Neuenschwander 1975, 1976), increasing the possible use of this species as biocontrol agents when other predators and parasites are still in diapause. H. pacificus played an important role in reducing aphid populations during lower temperature conditions in California (Neuenschwander and Hagen 1980). Apparently, temperature did not affect consumption rates on a related predator, Micromus variengatus (F.), a predator of Acyrthosiphon pisum (Harris) (Dunn 1954).

III. HEMEROBIUS STIGMA STEPHENS

Hemerobius stigma Stephens is widespread throughout Europe and is one of the most common species of Neuroptera in the British Isles (Killington 1937). Carpenter (1940) considered H. stigmaterus Fitch the most widely distributed species of Hemerobius in the Nearctic region.

Due to the similarities of adult genitalia, Tjeder (1960) synonymized H. stigmaterus with H. stigma and compiled a list of synonyms. Nakahara (1965) concluded that differences in the aedeagus might be important, and suggested that further studies involving dissections of a large number of specimens was necessary before establishing synonymy of the two species. However, most workers accept H. stigma as the senior synonym (Flint, personnel communication). In Europe, H. stigma is exclusively associated with conifers (Killington 1937). Nearctic populations are associated with a broader range of host plants. Smith (1923) collected H. stigma from Malus sp. and Trifolium sp. Along with conifers as a host, Throne (1971) recorded H. stigma on Quercus spp., Salix spp., Ostrya virginiana (Mill.) K. Koch, Hamamelis virginiana L. and Pyrus malus L. Also, Jubb and Masteller (1977) found H. stigma associated with Vitis labrusca L. in vineyards.

Adults of H. stigma are distinguished from other species by a very narrow or absent median stripe on the pronotum and mesonotum. The male genitalia also provide a useful taxonomic characteristic. The forewings have five or more gradate crossveins, and many specimens have a rufous pterostigma on both the forewing and hindwing. Color and markings are a function of season with summer forms having reddish-brown wings practically devoid of markings while winter specimens have gray-brown wings with several maculations (Withycombe 1922, 1923). Wing maculations and color of pterostigma are variable and not always a satisfactory diagnostic feature (Carpenter 1940). The species overwinters as either "prepupae" (Laidlaw 1936), pupae, or adults (Withycombe 1922, 1923; Killington 1937). Records of the Nearctic species indicate that adults occur from March to October and several

specimens were collected "in snow" in January. Oviposition occurs during warm periods in the winter in England (Killington 1937), and successive broods were recorded throughout the year (Withycombe 1922, 1923; Killington 1937). Only two broods a year occur in Scotland (Laidlaw 1936).

Eggs are deposited singly or in groups of 2-7 on the tips of the pine needles, under the scaly sheath at the base of a needle, and occasionally on twigs (Withycombe 1922; Killington 1937; and Miller and Lambdin 1982). Females begin laying eggs 3-7 days after emergence (Withycombe 1922), and one female was recorded as producing 86 eggs (Laidlaw 1936). Adults live "for at least eight weeks" (Withycombe 1922).

Egg morphology was described by Withycombe (1922, 1923), Smith (1923), Killington (1937) and Miller and Lambdin (1982). Miller and Lambdin (1982) determined that the "spots" and "pits" described by early workers were irregular-shaped, waxlike projections. They provided a detailed description of the micropylar process and coloration changes of the egg prior to eclosion.

External morphology of the developmental stages was recorded by Withycombe (1922, 1923), Smith (1923) and Killington (1937). Withycombe (1923) believed that the markings in the head and body of the second and third instar larvae were the same. Because of the similarity, Smith (1923) found it difficult to distinguish the instars. Duration of the developmental stages was detailed by Withycombe (1922, 1923), Smith (1923), Laidlaw (1936) and Killington (1937). Withycombe (1923) described rearing temperatures for the various stages.

Fully fed third instars seek a suitable site to spin a cocoon. Withycombe (1923) and Killington (1937) found cocoons of H. stigma

spun between two or three needles or in a crevice of tree bark. Douglas-fir cones provide an ideal pupation site adjacent to the larval feeding area for H. stigma and various other hemerobiids (Deyrup and Deyrup 1978). They reared 435 adult H. stigma from 700 fallen cones, and found that trees heavily infested with aphids may have at least one H. stigma cocoon per cone.

It is difficult to maintain larvae throughout their life cycle on diets of various aphids from apple, spiraea, snowball, cabbage, elm, and pine (Smith 1923). He also reported that larvae will canibalize eggs and larvae. H. stigma larvae will eat any species of aphid, but fare better on Aphis fabae (= rumicis) (Withycombe 1923). Eggs and larvae have also been associated with Adelges cooleyi, A. viridis, Lachnus pini, and Neomyzaphis abietina (Laidlaw 1936). He found one larva consumed approximately 3,000 eggs and newly hatched nymphs of A. cooleyi, one female adult consumed 17,588 Adelges and one male consumed 13,594 Adelges.

Parasites of Palearctic specimens include Anacharis ensifera Walk., Gelis ruficornis Thbg., (Withycombe 1923) and Hemateles areator Panz., (Killington 1932). Prior to 1978 there was only one record of a parasite of Nearctic Hemerobius (Muesebeck et al. 1951); Deyrup and Deyrup (1978) recorded ichneumonids of the genus Charitopes, figitids of the genera Anacharis and Aegilips, and specimens of an unidentified ceraphronid as parasites of Hemerobius.

CHAPTER III

MATERIAL AND METHODS

I. LABORATORY REARING

A laboratory colony of *H. stigma* was established 3 March 1981 at The University of Tennessee, Knoxville, from adults collected on white pine, *Pinus strobus* L., on the agricultural campus. The colony was maintained through August 1982 at 18.3° C ± 1.0° C, 60-80% RH, on 8L:16D, under incandescent and fluorescent light, in Percival I-35 and E-54U growth chambers. These environmental conditions were similar to those used by Neuenschwander (1975).

Forty-two male-female pairs were placed in 3.5 × 9.5 cm petri dishes for mating. The bottom of each petri dish was lined with a 9.0 cm disk of Fisher brand coarse filter paper. A 100 dr vial filled with distilled water and plugged with cotton was placed in each petri dish for water and moisture. A small piece of modeling clay was used to prevent the vial from rolling. A cotton ball, ca 1.5 cm diameter, and pine needles were placed in the dish to serve as ovipositional substrates. All immature stages were maintained under similar conditions in Falcon 1.0 × 5.0 cm culture dishes. Adults were fed white pine aphids, *Cinara strobi* (Fitch); cabbage aphids, *Brevicoryne brassicae* (L.); green peach aphids, *Myzus persicae* (Sulzer); woolly apple aphids, *Eriosoma lanigerum* (Hausman); and honey. Immatures were fed white pine aphids.

II. LIFE HISTORY

Adults were maintained until death to determine longevity, feeding behavior, fecundity and ovipositional habits. Eggs were collected within 24 hours after oviposition and weighed using an Ainsworth SCV electrobalance. Eggs were measured with an ocular micrometer. Egg color was compared to the color charts in the Munsell Book of Color (1929), and color description and incubation time were recorded. Larval molts were verified by discarded exuviae every 24 hours. Ten representatives for each larval stage were weighed to determine weight at ecdysus. Prepupal stage occurred when the larva spun a cocoon or bent its head, prothorax, and tip of abdomen in a ventrad position. Pupal stage was determined by the development of wing pads, compound eyes, and long antennae.

III. CONSUMPTION RATES

Twenty-four larvae were provided "unlimited" aphids daily. "Prey units" (New 1975) recorded as consumed daily were those aphids visibly "deflated" or sucked dry. Data was recorded as averages followed by ranges in parentheses.

IV. EXTERNAL MORPHOLOGY

Larval H. stigma were either preserved in 70% EtOH or mounted on slides using the technique described by Lambdin and Kosztarab (1977) for soft-bodied insects. Morphological measurements for the different larval stages were made using a Wild Heerbrugg phase contrast microscope

and recorded. Measurements were recorded in micrometers as averages followed by ranges in parentheses. A composite illustration was made for the larval stages. SEM photographs of eggs were used to determine the ultrastructure of the chorion.

V. PARASITES

Parasites of H. stigma were reared from field-collected larvae and maintained on honey. Development time for larval, pupal, and adult stages were recorded and ovipositional habits were observed. Larval, pupal, and adult stages were illustrated.

CHAPTER IV

RESULTS AND DISCUSSION

I. EXTERNAL MORPHOLOGY OF EGG AND LARVAL STAGES

Egg. Eggs were ellipsiod (Figure 1A), 730 (675-750) long, 335 (300-375) wide, and weighed 0.046 mg. Chorion surface irregular shaped, with waxlike projections evenly spaced on a smooth chorion (Figure 1B). These projections form diagonal patterns around the egg except where egg is attached to substrate. Projections near anterior pole fuse to encircle the micropylar process, those directly adjacent to the micropyle are connected by narrow waxlike bridges similar to those on the chorion of Chrysopa carnea Stephens (Mazzini 1976).

The micropylar process nipple-shaped, with irregularly shaped tubercle-like projections grouped into sections by fissures (Figure 1C). Narrow bridges proximally located interconnect each tubercle with adjacent tubercle, and each tubercle with centrally located aperture.

Taxonomic application of the egg. Mazzini (1976) noted that ultrastructural morphology of the egg chorion and micropyle has provided information useful for inferring phylogenetic relationships for insects in several orders. The chorion sculpturing is a sufficient characteristic to make a generic determination possible for some hemerobiids (Killington 1936). Additional comparitive studies may reveal that ultrastructure of hemerobiid eggs is diagnostic at the species level.

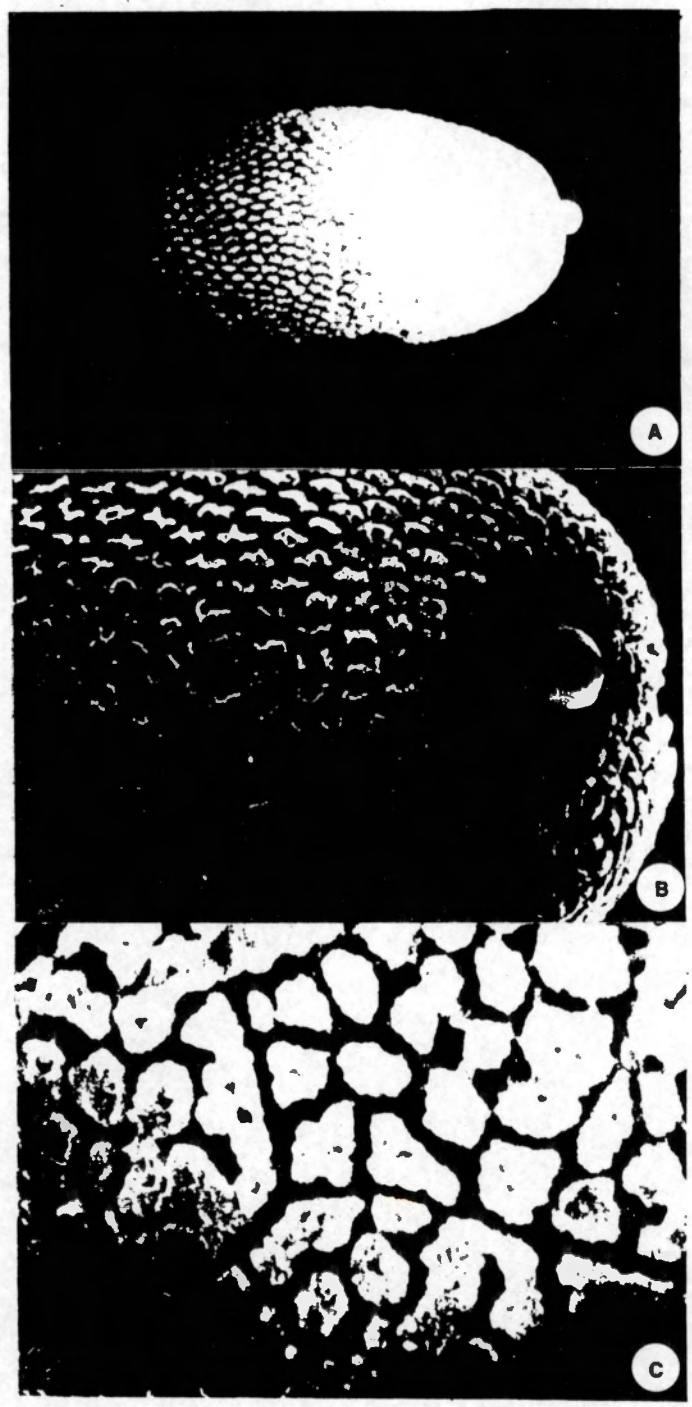

Figure 1. Egg of Hemerobius stigma Stephens. A, Egg of Hemerobius stigma (116×); B, Surface of anterior pole showing waxlike projections and micropylar process (144×); C, Tubercles and fissures on the micropylar surface (1200×).

Larvae. Body and head capsule size are not consistent characters to rely on due to size overlap of the instars. Empodia of the first instar larvae and the differences in chaetotaxy of the tenth abdominal segments between second and third instars provide ways to distinguish the instars. This contradicts Withycombe's (1923) belief that chaetotaxy was a useless character. A close examination of other species may reveal setae that are useful in differentiating species of Hemerobiidae.

Third stage larva. (Figure 2) Length 6,450 (4,600-7,200); width at metathorax 1,230 (860-1,440). Head capsule length 549 (435-600), width 495 (480-525). Head prognathous (Figure 2B), Y-shaped ecdysial suture articulated with antennal base; frons deltoid, with 4 pair of setae. Genae with 4 setae in oblique row, 3 tacklike setae and a campaniform sensillum on posterior margin of sclerite, 2 setae on lateral margin near 3 ocelli, and 2 setae on venter. Antenna 3-segmented; scape 97 (90-120) long, 90 (75-105) wide; pedicle 63 (60-69) long, 54 (42-60) wide; pedicle 63 (60-69) long, 54 (42-60) wide; flagellum 531 (510-555) long, with 4 pair of tacklike setae and a needlelike apical seta. Maxilla with 2 longitudinal rows of 6 (6-9) needlelike setae; apically, with 6 (6-8) tacklike setae, 4 (3-4) spinelike setae on outer margin, and 2 needlelike setae on inner margin. Submentum with 3 lateral setae, prementum with 2 ventral setae. Labial palpus 3-segmented, 1 pair of needlelike, 1 tacklike seta and sensory pore on first segment; 1 pair of setae and two sensilla on second segment; a circulet of 18-20 spines at apex and a sensillum on anterior third of third segment.

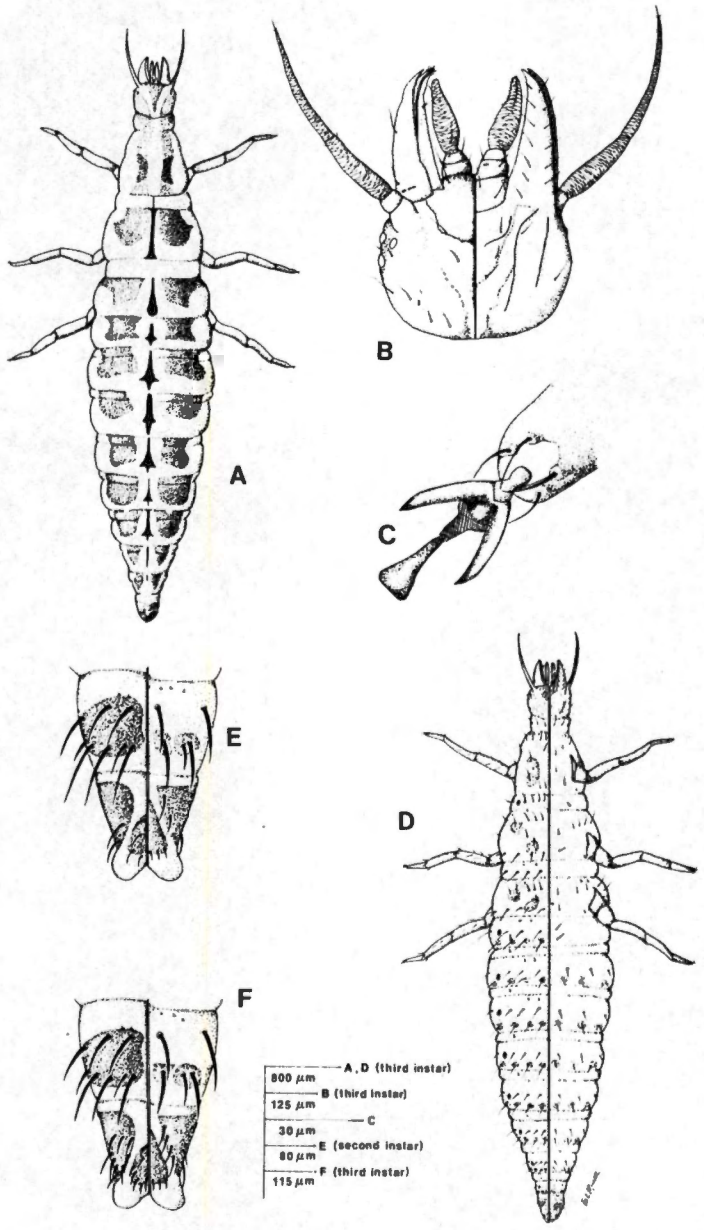

Figure 2. External morphology of the larval stages of Hemerobius stigma Stephens. A, Hemerobius stigma, third stage larva dorsal habitus; B, Dorsal and ventral head region of first, second, and third stage larvae; C, Tarsus of first stage larva; D, Chaetotaxy of dorsum and venter of third stage larvae; E, Dorsum and venter of abdominal segments 9 and 10 for first and second stage larvae; F, Dorsum and venter of abdominal segments 9 and 10 for third stage larva.

Each thoracic segment divided into 2 subequal annulets; integument covered with minute spinules. Prothorax: Dorsum of anterior annulet with 3 setae in transverse row; venter with 3 tacklike setae on anteriolateral margin and 3 needlelike setae in transverse row on each side. Dorsum of posterior annulet with 3 tacklike setae on anteriolateral margin, 3 needlelike setae on lateral margin, 4 needlelike setae in transverse row anteriorly, and 2 needlelike, and 1 spinelike submedial setae. Pair of submedial kidney-shaped sclerites, dorsum of each with a needlelike and spinelike seta, an anterior margin and a medial needlelike seta; venter with 3 tacklike setae on anteriolateral margin and 6 (4-6) setae arranged in 2 oblique rows in submedial area. Mesothorax: Dorsum of anterior annulet with a transverse row of 5 needlelike setae and a lateral spiracle; venter with a pair of spinelike setae. Dorsum of posterior annulet with a tacklike seta on anteriomedial margin, 3 needlelike setae on lateral margin, 3 needlelike setae in transverse row anteriorly, anterior submarginal chalaza with 2 needlelike and 1 spinelike setae; 1 needlelike submedial seta and 2 needlelike setae on posterior margin with a posterior rounded sclerite with a medial needlelike and anterior tacklike seta; venter with a circulet of 4 needlelike setae on anteriolateral margin, 2 needlelike setae medially and 1 tacklike seta on submargin of posterior. Metathorax: Dorsum of anterior annulet with 4 needlelike setae in transverse row and 2 tacklike setae on anteriosubmargin; venter with microspines only. Dorsum of posterior annulet same as posterior annulet of mesothorax, but only 1 needlelike seta on posteriolateral margin; venter with same pattern as mesothorax except 2 spinelike setae on anteriomedial margin.

Abdomen: (Figure 2D) 10-segmented, each segment membranous, divided into 2 subequal annulets except first segment with 1 annulet, each annulet with numerous microspinules. Dorsum of first segment with marginal spiracle, two tacklike setae and a transverse row of 4 needlelike setae anterior; 4 chalazae posteriorly located, setal arrangement from lateral margin to midline 1-2-1-2 alternating spinelike and needlelike; venter with 2 spinelike submedial setae. Dorsum of anterior annulet of segments 2-7 with a submarginal tacklike seta on each half; venter with microspinules only. Dorsum of posterior annulet of segments 2-7 same as first segment; venter with transverse row of 3 needlelike setae anteriorly and a transverse row of needlelike and spinelike setae arranged 2-1-1 from lateral margin to midline posteriorly. Dorsum of anterior annulet of segment 8 with submarginal tacklike seta; posterior annulet same as above except anteriorly with 3 needlelike setae and posteriorly with 3 chalazae, setal arrangement on chalazae from lateral margin to midline 2-1-2. Venter of posterior annulet with 3 tacklike and 1 needlelike medial setae, and 1 needlelike seta on lateral margin anteriorly; transverse row of chalazae arranged 2-1 from margin to midline posteriorly. Segment 9 (Figure 2F) with same setal pattern as 8 but more heavily sclerotized and without lateral spiracles. Segment 10 without setae on anterior annulet, but with a lateral and medial sclerotized plate on posterior annulet; lateral plate with 9 (8-9) needlelike and spinelike setae on lateral, medial, and posterior margins of sclerite; medial sclerite deltoid with 14 (12-16 spinelike setae. Ventrally, no setae on anterior annulet; posterior

annulet with two sclerites, lateral sclerite with oblique row of 7 needlelike and spinelike setae; medial deltoid sclerite with transverse row of 6 spinelike setae on posterior margin.

Second stage larva. Length 3,660 (3,060-4,840); width at metathorax 680 (580-900). Head capsule (Figure 2B) length 369 (339-384), width 381 (366-390). Antennae 3-segmented, scape 75 (60-90) long, 63 (54-72) wide; pedicel 42 (36-51) long, 42 (36-45) wide, flagellum 405 (375-429) long. Segmentation and chaetotaxy similar to third instar with following exceptions: Prothorax—venter of posterior annulet with an additional tacklike seta on anterior lateral margin. Mesothorax: venter of anterior annulet with only a tacklike seta on anterior submargin. Abdomen: posterior annulet of segment 10 (Figure 2E) with dorsolateral sclerite possessing 2 needlelike setae in oblique row on posterior margin, dorsal deltoid sclerite with a longitudinal row of 4 pair of longitudinal needlelike setae; venter with lateral sclerite possessing 3 needlelike setae in oblique row on posterior margin.

First stage larva. Length 2,440 (1,440-3,200), width at metathorax 460 (200-600). Head capsule length 288 (219-360), width 315 (270-375); antennae 3-segmented, scape 57 (30-62) long, 54 (36-81) wide, pedicel 39 (27-45) long, 39 (33-45) wide; flagellum 339 (330-357) long. Tarsi (Figure 2C) with trumpet-shaped empodia. Segmentation and chaetotaxy similar to third instar with following exception: Prothorax—Dorsum and venter of anterior annulet without transverse row of setae. Dorsum of posterior annulet lacking anterior transverse row of setae; venter

with a tacklike seta on posterior submargin. Dorsum of posterior annulet lacking anterior transverse row of setae, only 1 needlelike seta on posteriolateral margin; venter with a tacklike seta on posterior submargin only. Mesothorax: Dorsum of anterior annulet lacking transverse row of setae; venter with only a tacklike seta on posterior submargin. Dorsum of posterior annulet lacking anterior transverse row of setae, with 1 needlelike seta on posteriolateral margin; venter with 2 tacklike setae on anteriolateral margin, and 1 needlelike seta medially and 1 spinelike seta on posterior submargin. Metathorax: Dorsum of anterior annulet lacking transverse row of setae; venter with only a tacklike seta on posterior submargin. Dorsum of posterior annulet lacking anterior transverse row of setae; venter with 2 tacklike setae on anteriolateral margin, 1 needlelike seta medially and 1 spinelike seta on posterior submargin.

Abdomen: posterior annulet of segment 10 (Figure 2E) with dorsolateral sclerite possessing 2 needlelike setae in oblique row on posterior margin, dorsal deltoid sclerite with a longitudinal row of 4 pair of needlelike setae; venter with lateral sclerite possessing 3 needlelike setae in oblique row on posterior margin.

II. KEY TO THE LARVAL STAGES OF HEMEROBIUS STIGMA STEPHENS

1. Tarsi without trumpet-shaped empodia 2

   Tarsi with trumpet-shaped empodia . . . . . first stage

2. Posterior annulet of segment 10 with 2 needlelike setae in oblique row on medial margin of

dorsolateral sclerotized plate; lateral sclerite on venter with 3 needlelike setae on oblique row on posterior margin . . . . . second stage

Posterior annulet of segment 10 with 8-9 needlelike and spinelike setae on medial and posterior margins of dorsal and lateral plates; lateral sclerite on venter with 7 needlelike and spinelike setae in oblique row on posterior margin . . . . . third stage

III. LIFE HISTORY

Field observations. Female H. stigma deposited eggs on pine needles, on the scaly sheath at the base of the needles, and occasionally in a crevice on a pine bough. I observed eggs on the same branch as the eggs of C. strobi. Larvae of H. stigma fed on C. strobi and pine leaf adelgids, Pineus pinifoliae (Fitch). Larvae curl around the terminal bud and insert their mouth parts into the wooly wax of P. pinifoliae. I found pupal cocoons in tree bark crevices and pine cones, and February 25, 1982, collected 29 cocoons from 42 cones of Virginia pine, Pinus virginiana Mill. H. stigma adults were observed on blue spruce, Picea pungens Engelm.; Virginia pine, P. virginiana; and white pine, P. strobus. This collection represents a new county and state record for distribution of the species.

Adults never remained in sustained flight for long distances and usually flew to adjacent branches. Adults continually waved their

antennae as they traversed the needles and branches. One female oviposited in the scaly sheath at the base of a pine needle and one adult ate an unidentified psyllid. When adults were disturbed, they feigned death and fell to the ground or lower branches. Wings of one H. stigma were found in a spider's web on white pine.

Laboratory studies. Females deposited eggs singly or in groups of 2-5 on filter paper, cotton balls, pine needles, on the scaly sheath at the base of the needles, and in a mummy of a cabbage aphid, B. brassicae, (Figure 3). Eggs 1-3 days after deposition were yellow (5 Y 8/6), changing to yellowish red (10 YR 7/6) after four days, darkening (10 YR 7/8) with embryonic development until hatching after about five days. Hinton (1981) concluded that many insect eggs undergo coloration change during incubation due either to a change in color of the chorion or to a color change of the embryo as seen through the eggshell. The maturing embryo caused the apparent color changes in the chorion of H. stigma eggs. Ninety-eight percent of the eggs (n = 174) were viable. Incubational time was 4.6 (2-7) days (Table 1).

Duration of the larval stages based on observations of C. strobi fed larvae (Table 1) was: first, 4.3 (2-10) days; second, 4.0 (2-7) days; and third, 7.8 (4-16) days. Larvae successfully molted only on a diet of C. strobi. When cabbage aphids, B. brassicae; green peach aphids, M. persicae; woolly apple aphids, E. lanigerum; and greater wax moth larvae, G. mellonella were provided, they were rarely attacked. These regimens produced 100% mortality in H. stigma with no larvae molting past the prepupal stage. Laidlaw (1936) related that waxy secretions

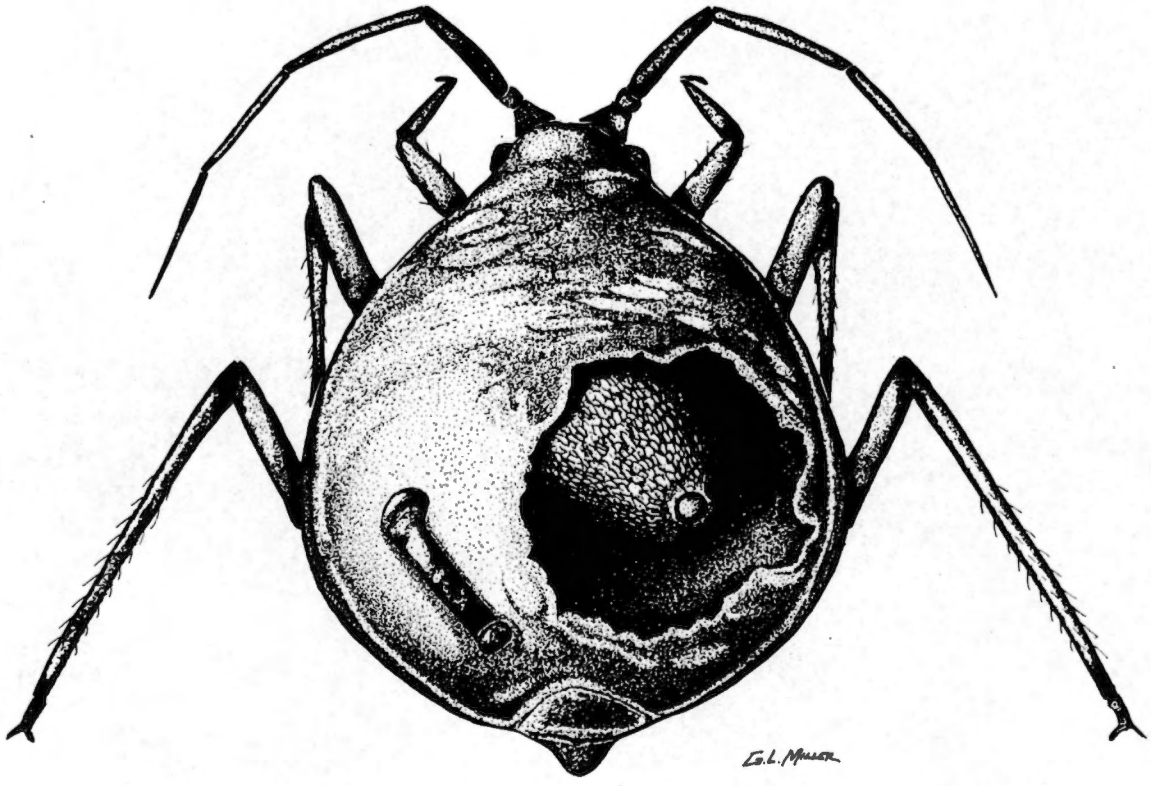

Figure 3. Egg of Hemerobius stigma in a mummified cabbage aphid, Brevicoryne brassicae.

Table 1. Development of immature and adult stages of Hemerobius stigma Stephens.

Stage	Number of Observations	Duration in Days		Cumulative Mean Age
		Range	Mean	
Egg	174	2- 7	4.6	----
Larval				
First	79	2-10	4.3	4.3
Second	76	2- 7	4.0	8.3
Third	75	4-16	7.8	16.2
Prepupal[1]	70	3-12	6.2	22.4
Pupal[2]	69	8-15	11.2	33.4
Adult				
Male	24	1-59	25.1	58.5
Female	31	1-77	40.7	74.1

[1]Duration of pharate pupal stage was not determined.

[2]Duration of pharate adult stage was not determined.

of some prey were a constant feeding obstruction for H. stigma larvae, which may partly explain why B. brassicae and E. lanigerum were not suitable prey. These observations contradict Balduf's (1939) belief that hemerobiid larvae feed on any soft-bodied insect. It indicates that H. stigma may be more prey specific than previously thought (Withycombe 1922), and may explain why Smith (1923) had difficulty rearing this species.

Larvae crawl on all sides of the rearing containers in search of prey. They use their pygopods as an accessory walking structure and swing their heads from side to side while walking. The ventral side of each maxillae has a double row of setae which probably aid in food detection and cause the "head swinging" that typifies this family.

Larvae would often overlook potential prey unless they made direct contact. After the larva inserts its mouthparts, it lifts the prey by tilting its head back and raising its pronotum with its forelegs. The last abdominal segment serves as a "hold fast" structure and the antennae are held perpendicular to the body (see Figure 4). When prey is encountered near the side of the container, the larva crawls backwards and up the side of the container. The larva keeps its head and prey almost perpendicular to the base of the container and continues to feed utilizing its pygopod and bracing itself with the forelegs. Consumption rates of the larval stages were recorded as: first stage, 6.0 (2-13); second, 5.4 (2-14); and third, 44.7 (13-62) white pine aphid prey units. A third instar larva, unfed for two days was observed to consume eight prey units in one hour before it stopped searching for prey. These

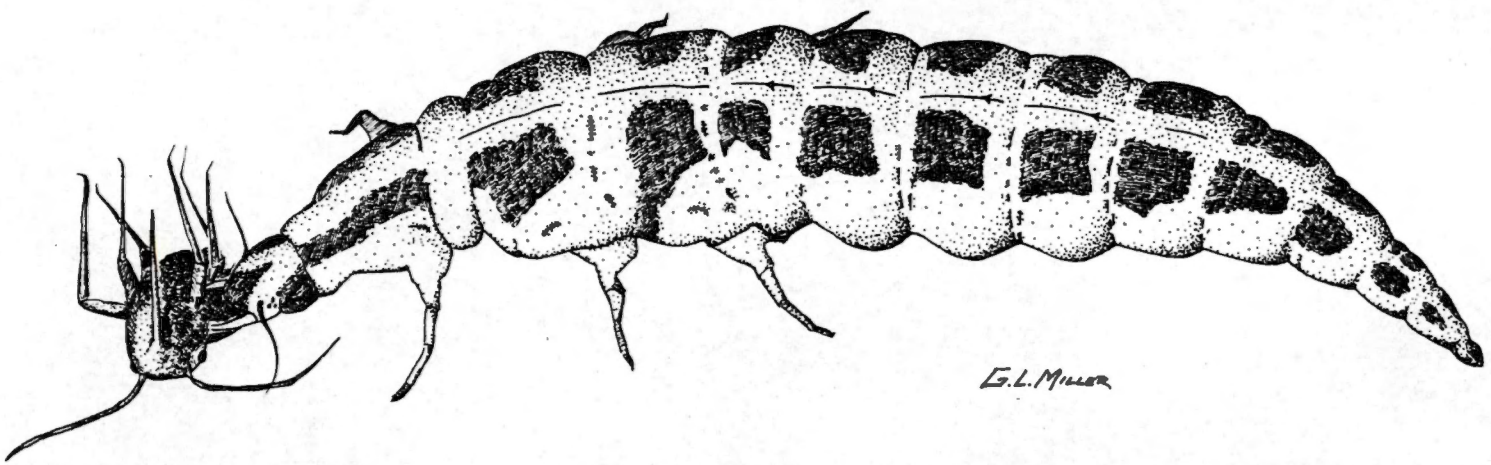

Figure 4. Hemerobius stigma feeding on a white pine aphid, Cinaria strobi.

consumption rates are considerably less than Laidlaw's (1936) observations of 3,000 A. cooleyi consumed for one larva of H. stigma, but consideration of size variation and biomass of A. cooleyi versus C. strobi must be given.

After feeding, the larvae sometimes rubbed both sides of their heads on the substrate and attacked the aphid they had just fed upon. Larvae probed all cast aphid skins and dead aphids encountered including their own. Weight ranges for the larval stages at eclosion were: first stage, 0.035 (0.017-0.057) mg; second stage, 0.288 (0.100-0.450) mg; and third stage, 1.471 (1.100-2.00) mg.

Once third instar larvae were fully fed, they entered the prepupal stage. Only 18.3% of the third instars spun the typical hemerobiid cocoon. Smith (1923) reported that some larvae do not spin cocoons but undergo transformation outside a cocoon. The prepupal stage was determined to last 6.2 (3-12) days (Table 1, page 24).

The pupal stage of H. stigma lasted 11.2 (4-15) days (Table 1). Upon emergence, the papa's antennae, wing pads and eyes darken. After emerging from the pupal exuvia, the adult positions itself on the side or top of the container and expands its wings. A meconial pellet (Figure 5) is then deposited in the container. The pellet was 1550 (1300-1690) long and 500 (400-560) wide, elongated with rounded ends, surface rugous, indistinctly annulated and covered with silken strands. Debach et al. (1978) related that meconial characteristics may serve as an important systematic tool. Twenty-two percent of the observed pupae did not complete successful ecdysis. The mortality may be due

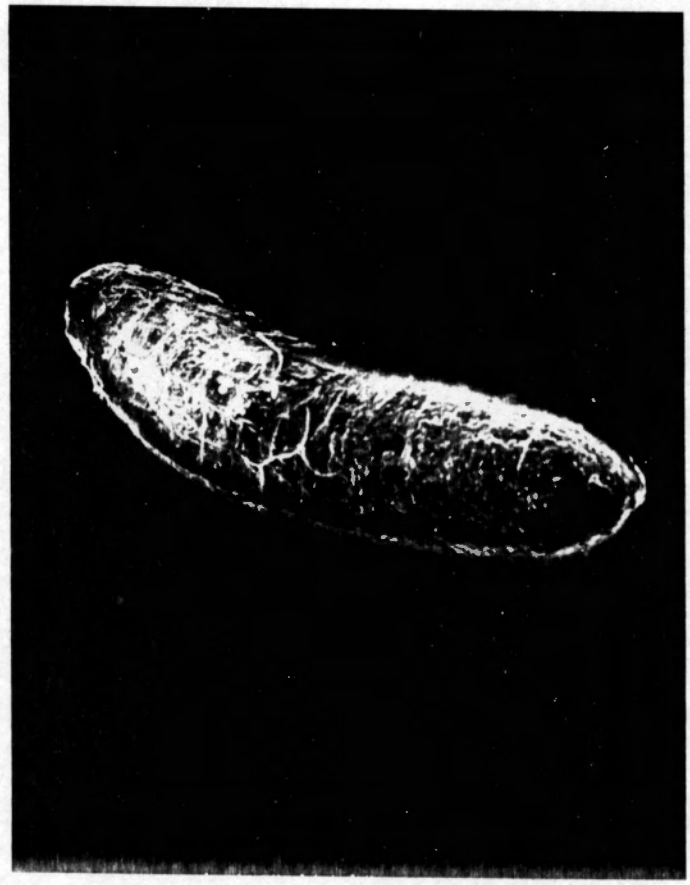

Figure 5. Meconial pellet of Hemerobius stigma (416×).

to lack of a suitable substrate for the pupa to molt. The sex ratio of emerged adults was: 44% males and 56% females.

H. stigma adults could be maintained on numerous aphids that the larvae would not eat. Feeding behavior included direct contact with the prey. Antennae could touch the prey, but this action did not always initiate a feeding response. The palpi seem to play an important role in prey detection. An adult probes an object with the apiculus of the palpus, determines whether it is suitable prey, and attacks. The legs of aphids were usually probed first. The adult would then chew off part of the leg and attack the body of the aphid. Adults would not always finish feeding on an aphid before attacking another prey.

Adult longevity for laboratory reared specimens was 25 (1-59) days for males and 40.7 (1-77) days for females (see Table 1, page 24). Mating behavior was not observed, but Carpenter (1940) related that copulation takes place at night. Male-female pairs would often touch antennae but any movement of one adult toward the other resulted in aggression. One adult was observed to chew off part of the antenna of another adult after an encounter as above.

Females laid an average of 194 (0-827) eggs. The female would tap the surface with her palpi and wave her antennae as she traversed the substrate. When a suitable position was found, she turned, arched her abdomen and deposited an egg. Elapsed time to deposit an egg was about 2-3 seconds. One female was observed to bend the tip of her abdomen to her mouth and eat the egg about to be delivered. They laid eggs (n = 192) on pine needles (49%); cottonballs (31%); the scaly sheath of the needles (10%); and on folds of paper (9%).

Parasites. Two females (Figure 6), Anacharus sp. (Figitidae), were reared from two field collected H. stigma larvae. Parasites consistently tapped the substrate with their antennae. When it neared a H. stigma larva, it would palpate the hemerobiid a few times, then hold its wings aloft, bend its abdomen between its legs and insert the ovipositor into the center of the hemerobiid's dorsum. One H. stigma larva was observed to rear back and "snap" at the parasite, then run off with the female ovipositing as it moved. Only late second stage and third stage larvae are attacked while prepupae and pupae are ignored. After 7.5 (6-9) days, the larval parasite (Figure 7A) eats its way through the cuticle of the prepupal host. The exocorporal stage lasts 5.3 (3-8) days; the pupal stage (Figure 7B) lasts 7.3 (4-10) days. Total development time was recorded as 20.4 (19-21) days from oviposition until adult emergence. Adult longevity for field collected specimens was 15.5 (6 and 25) days while laboratory reared specimens was 10.5 (4-23) days.

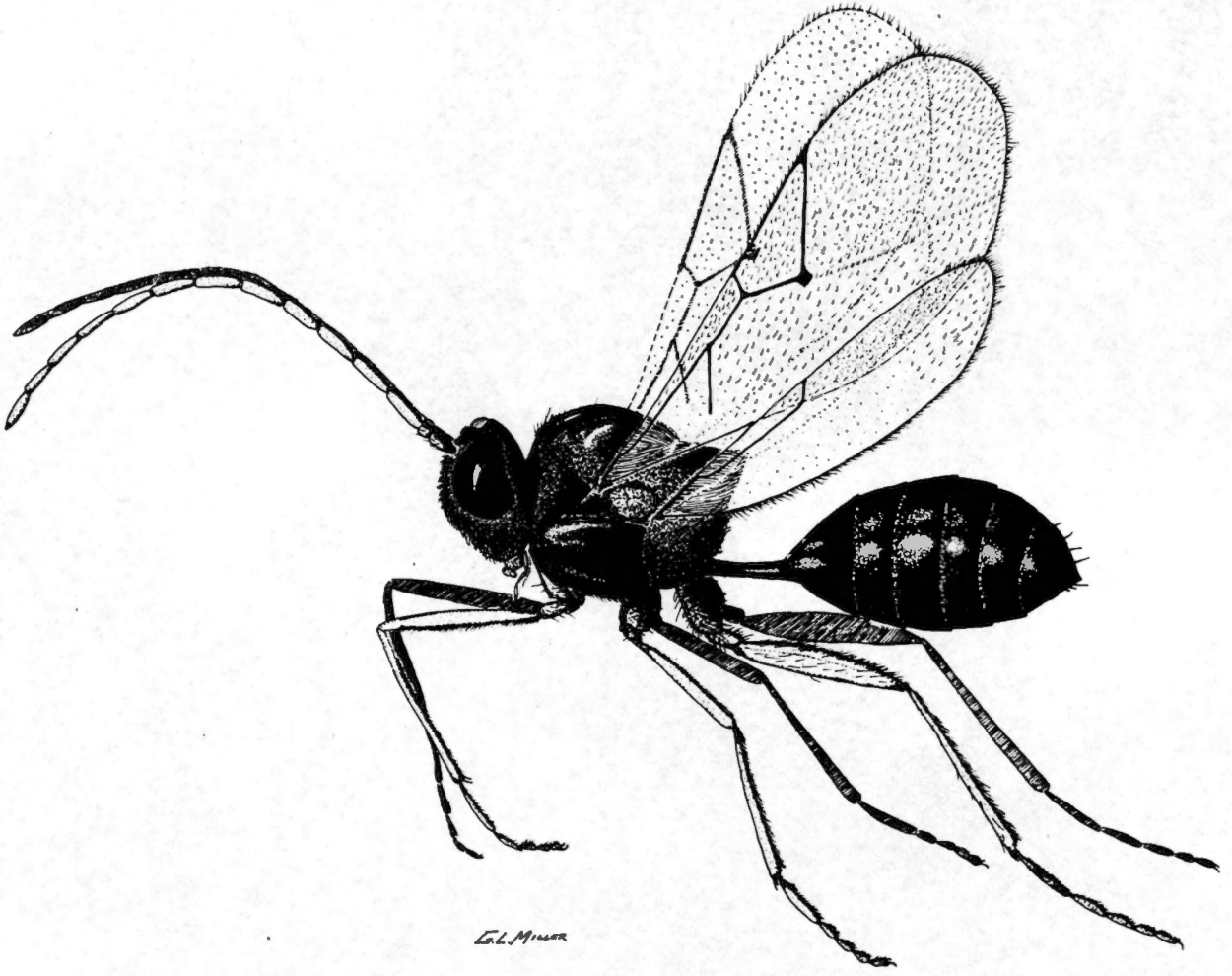

Figure 6. Anacharus sp., female, lateral habitus.

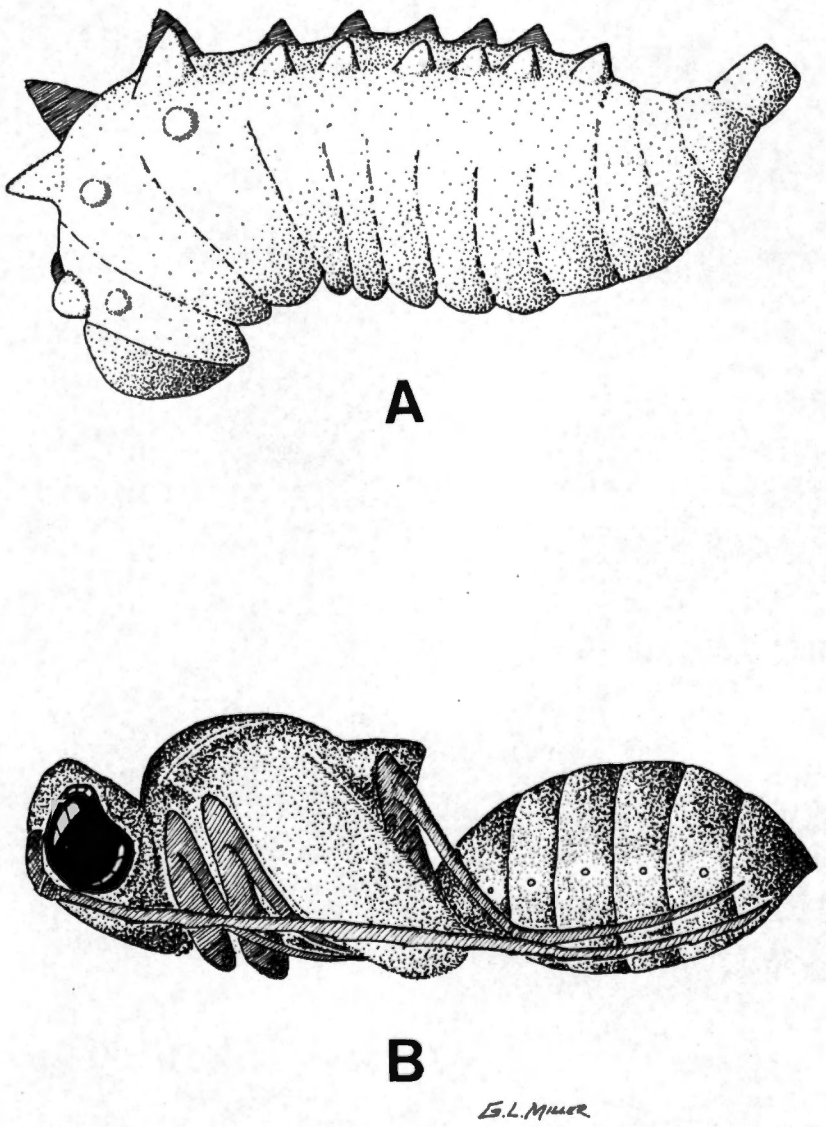

Figure 7. Larval and pupal stages of Anacharus sp. A, Last larval stage of Anacharus sp.; B, Pupal stage.

CHAPTER V

CONCLUSIONS

Because the waxlike projections on the surface of the chorion and micropylar process are consistent for eggs of H. stigma, the pattern may be significant in species determination. In addition, adult meconial pellets, when combined with other factors, may afford useful taxonomic characters. Larval chaetotaxy can be used to distinguish the immature stages, specifically those setae on the dorsum of the thorax and tenth abdominal segment. Also, first stage larvae differ from second and third stage larvae by possessing empodia. Similar studies on Palearctic species may provide information on phylogenetic relationships.

Larvae of H. stigma are more prey specific than originally considered by earlier investigators. This could explain the difficulty encountered in rearing a laboratory population on anything other than aphids associated with conifers. On a diet of C. strobi, the most critical stage is the pupal stage where a mortality rate of 22% occurs.

Although its usefulness on agricultural row crops may be debatable due to high larval mortality, H. stigma's usefulness as a biocontrol agent on conifers is highly possible. H. pacificus was determined to be a cold weather predator by Neuenschwander and Hagen (1980); thus, H. stigma may also play an important role in suppressing pest populations under cold weather conditions.

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VITA

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