CATERPILLARS of EASTERN NORTH AMERICA

A GUIDE TO THEIR IDENTIFICATION AND NATURAL HISTORY

DAVID L. WAGNER

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UNITED STATES FOREST SERVICE FHTET PROGRAM AND DISCOVER LIFE IN AMERICA

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Dedication

To my children Virginia and Ryan, wellsprings of pint-sized adventures, good times, and fond memories, I dedicate this work

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PREFACE

I recently attended a seminar at Harvard University to hear Stefan Cover speak. He started off simply enough. “Everyone needs an obsession. Mine is ants.” Everyone chuckled … more than a few heads nodded in agreement. For the past ten years mine has been caterpillars. They have provided a bounty of trip memories, abundant photographic opportunities, led to dozens of collaborations and friendships, some of which will be lifelong, and introduced me to a world full of beauty, change, carnage, and discovery. Stefan was right.

My goal in writing this guide is twofold. First, to provide larval images and biological summaries for the larger, commonly encountered caterpillars found east of the 100th meridian. Sounds simple, yet the problems associated with compiling such information are legion: literature is scattered, lacking, or, worse, especially in the case of some early accounts, wrong. For many common moths the species taxonomy is still under study, life histories are incompletely known, and distributional data have yet to be assembled. In this guide I offer a synopsis for each species that includes information on its distribution, phenology, and life history. Taxonomy has been updated, (Eastern) distributions adjusted, and information on the number of annual broods added for many of the species treated in Covell (1984), the “go to” book for Eastern moths. In addition, numerous caterpillars are illustrated here for the first time, dozens of new foodplant records are presented, and considerable previously unpublished life history information has been provided. But I caution that each species treatment is only a first step and that many accounts will require revision as our fauna becomes better known. Behaviors and phenomena previously believed to be exceptional or uncommon are shown to be otherwise: e.g., both Batesian and Müllerian mimicry appear to be more prevalent in caterpillars than previously recognized. Pronounced developmental changes (in form, coloration, and behavior), bordering on hypermetamorphosis, were seen in several families—striking examples occur among the daggers and slug caterpillars. Inducible color forms, e.g., darker morphs in high density inchworm and hornworm populations, are more common and taxonomically widespread than has been generally recognized.

My second goal for this work is to showcase some of the insect life that is right outside one’s door or in nearby parks. Our National Forests and Parks are rife with biological riches. While it is almost a universal dream of biologists and weekend naturalists to someday explore a tropical rain forest, it is not necessary to be transported to a jungle to find beauty, view mysterious phenomena, or make new biological discoveries … all exist as close as the nearest woodlot. All that it takes is to walk more slowly, watch more closely, and develop a greater appreciation for what E. O. Wilson calls “the little things that run the world.”

This book was written so as to be understandable to a student in middle school but also detailed enough to provide new information to a seasoned museum curator, accomplished lepidopterist, applied entomologist, conservation biologist, or land manager. Admittedly the text bounces between these audiences, and awkwardly so at times … my apologies. Because the audience will be mixed, I usually list both common and scientific names even when it is disruptive to do so. Space limitations dictate that I adopt a mostly telegraphic style except in the Remarks section where full text is provided. The more I had to relate about a species, the more telegraphic the text.

I am not sure what brings me more pleasure: the hunt, rearing, or photography. I enjoy reading about a species, researching its foodplants and habits, planning a trip, and then searching for its caterpillar. There is great satisfaction in caterpillar rearing and wrangling: watching them eat, grow, and ultimately metamorphose into something often completely unexpected and strikingly beautiful. Caterpillars that appear drab and mundane at arm’s length often prove exquisite creatures when viewed through my camera’s macro lens. Taking images that justly render their beauty or capture aspects of their behavior is very rewarding. It is my wish that this guide will enable others to share in all of this sport and facilitate the efforts of those wishing to contribute to our knowledge of Eastern moths, because so much remains to be discovered and told.

ACKNOWLEDGMENTS

Much of the knowledge that sits behind this guide resides in the reviewers who read the species accounts and in the dozens who shared observations and contributed in other ways. In this regard a special debt of gratitude is owed to Dale Schweitzer who, above all others, served as my mentor and advisor. My colleagues and friends, Richard Heitzman, Steve Roble, Jadranka Rota, Fred Stehr, and Bo Sullivan read drafts of nearly every chapter. Others who reviewed chapters, roughly in order of number of species accounts read, include Dale Schweitzer, Richard Peigler, James Adams, David Wright, George Balogh, Ben Williams, Charles Covell, Noel McFarland, Eric Hossler, John Peacock, Jim Tuttle, Marc Epstein, John Lill, Paul Opler, Brian Branciforte, Jessica Lowrey, John Foltz, and Paul Schaefer. Michael Thomas and Kevin Fitzpatrick reviewed the section on photography; Judy Dulin that on school projects. James Adams, Jeff Boettner, Bonnie Drexler, Richard Heitzman, Eric Hossler, Jeff Lougee, Jane O’Donnell, Dale Schweitzer, Fred Stehr, Bo Sullivan, Jessica Watson, Ron Wielgus, and Ben Williams provided helpful suggestions on the book’s introductory sections.

Those who collected foliage daily, serviced the rearing lots, preserved vouchers, labeled specimens, kept records, and maintained the database played a quintessential part in this effort: Valerie Giles, Eric Hossler, Monty Volovski, Julia Joseph, Julie Henry, Susan Herrick, Jennifer Jacobs, and Brian Branciforte. Keith Hartan and Jadranka Rota pitched in on numerous occasions. The first three contributed hundreds, and perhaps thousands of hours beyond what I could afford to pay them—their commitment, enthusiasm, and friendship enabled all of this happen. I owe much to my friend Ben Williams who reared many egg lots to maturity and transported the fully grown caterpillars to the lab to be photographed.

Many colleagues sent gravid females, eggs, or caterpillars. First among these was Dale Schweitzer who has contributed livestock over the past decade. Numerous collections, roughly in order of the numbers of caterpillars that appear in this work, were made by Eric Hossler, Monty Volovksi, Ryan Wagner, Valerie Giles, Ben Williams, Mike Thomas, Doug Ferguson, Andy Brand, Jeff Fengler, and Bo Sullivan. Monty was especially enthusiastic and helpful, and on two occasions took vacation time to collect for this work. Smaller numbers of caterpillars were received from Laura Miller, Tom Allen, Paul Goldstein, Warren Kiel, Scott Smedley, James Adams, Michael Nelson, Julia Joseph, Teddy Lamb, Jenny Jacobs, Tim McCabe, Keith Hartan, Don Lafontaine, William Forrest, Paxton Mallard, John Peacock, Jadranka Rota, Paulette Haywood, Tom Hupf, Kate Kubarek, Jessica Lowrey, Jane O’Donnell, Virginia Wagner, George (Jeff) Boettner, Bryan Connolly, Fred Hohn, Chris Lamb, George Leslie, Nancy Lowe, William Oehlke, Kristian Omland, Ric Peigler, Dave Simser, Bob Wilson, George Balogh, Bill Conner, Jim Duquesnel, Donna Ellis, Julie Henry, Charlene Houle, Carol Lemmon, John Lill, Nam Nguyen, Carl Rettenmeyer, Linda Ruth, Brent Salazar, Juan Sanchez, Brian Scholtens, Justin Smith, Carolyn Bursey, Michael Canfield, Liz Day, Dave Doussard, Marc Epstein, Roy Kendall, Steve Talley, Gaines Taylor, and David Silsbee. Many others, too numerous to mention, passed along the occasional egg batch or caterpillar or two. This guide is built upon their efforts. Many of the above accompanied me on the innumerable trips that yielded the caterpillars that appear on these pages—I thank all for their companionship, enthusiasm, assistance, and memories now shared.

Several individuals contributed phenological and distributional data, foodplant records, personal observations, and other information: James Adams, George Balogh, Vernon Brou, Douglas Ferguson, Howard Grisham, Edward Knudson, Hanna Roland, and Bo Sullivan. Special thanks are due to Richard Heitzman who checked the range, phenology, annual broods, and foodplant records for all Missouri species that appear in this guide, and to Dale Schweitzer who generously offered his encyclopedic knowledge of moths and butterflies from start to finish. Identifications of parasites and pathogens were provided by Michael McAloon, Barry O’Connor, Ian Gauld, Scott Shaw, and David Wahl. Kathleen Tebo input many editorial changes and mailed chapters to and fro. Literature was sent by Larry Davenport, Dave Doussard, Richard Peigler, and Martha Weiss. Bryan Connolly, James Duquesnel, Les

Mehrhoff, and Ken Metzler helped out with botanical matters: providing identifications, collecting foliage, and/or sending directions to the nearest patch of this or that plant. Clint Morse supplied cuttings from the research plant collections at the University of Connecticut for several foodplants that could not be found near campus.

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PHOTOGRAPHIC AND ARTWORK CREDITS

Rene Twarkins took all the adult images and scanned the 1,200 larval images. More importantly, he dedicated hundreds of hours (and more than a dozen sleepless nights) to the image manipulations and management necessary for this book. His dedication to this effort, his expertise, and attention to detail are deeply appreciated. In the final weeks, Shawn Kennedy logged dozens of hours making necessary adjustments to all of the larval images. Valerie Giles contributed most of the line art. Shawn Kennedy prepared the wing coupling and arctiid crochets drawings. The majority of the images used in this guide were taken by me or those working in my lab. More than 75,000 images, not reproduced here, sit behind this work and are part of a photographic reference collection at the University of Connecticut. Over the four summers that Valerie Giles worked in the lab, she added thousands of images to this collection and kept the slides curated. Eric Hossler also contributed substantially to the collection of reference images. Don Lafontaine arranged the loan of many of the Canadian National Collection images. Those contributing the images that appear in this guide are listed below—their willingness to share these is gratefully acknowledged.

GEORGE BALOGH: *Proserpinus gaurae*; BOB BARBER: *Erynnis juvenalis* (insets); ANDY BRAND: *Composia fidelissima*; SARA BRIGHT: *Cyllopsis gemma*, *Neonympha areolata*; PAT BURKETT: *Harrisimemna trisignata*; DAVE DOUSSARD: *Trichoplusia ni*; JEFF FENGLER: *Anatrytone logan*, *Datana perspicua*, *Heterocampa umbrata*, *Libytheana carinenta*, *Parrhasius m-album*, *Protambulyx strigilis*, *Roddia vaualbum*, *Selenisa sueroides*; DOUG FERGUSON: *Acronicta oblinita*, *Cisthene packardii*, *Cisthene plumbea*, *Costaconvexa centrostrigaria*, *Crambidia pallida*, *Dasychira tephra*, *Datana contracta*, *Euchlaena obtusaria*, *Helicoverpa zea*, *Iridopsis pergracilis*, *Lycia ypsilon*, *Metanema determinata*, *Spodoptera frugiperda*, *Zale perculta*; WILLIAM FORREST: *Euxoa messoria*, *Haploa confusa*, *Haploa contigua*, *Haploa reversa*, *Peridroma saucia*, *Pyrrhia exprimens* (3), *Xestia badicollis* (3); VALERIE GILES: *Achalarus lyciades*, *Acronicta afflicta*, *Acronicta dactylina*, *Acronicta increta*, *Agrotis ipsilon*, *Alsophila pometaria* (inset), *Amphion floridensis*, *Anisota virginiensis*, *Anthocharis midea*, *Autographa precationis*, *Besma quercivoraria* (2), *Bombyx mori* (2), *Cabera erythemaria*, *Cabera variolaria*, *Callophrys gryneus*, *Callopistria mollissima*, *Callosamia promethea*, *Callosamia securifera*, *Calophasia lunula* (2), *Campaea perlata*, *Catocala antinympha*, *Catocala epione*, *Catocala insolabilis, Catocala muliercula*, *Catocala obscura*, *Catocala relicta* (2), *Catocala ultronia*, *Ceratomia amyntor*, *Clostera inclusa*, *Coryphista meadii*, *Crocigrapha normani*, *Cucullia convexipennis* (2), *Cucullia intermedia*, *Cyclophora pendulinaria*, *Cycnia tenera*, *Darapsa myron*, *Dasychira obliquata*, *Deidamia inscripta*, *Drepana arcuata*, *Epimecis hortaria*, *Eubaphe mendica*, *Euclea delphinii*, *Euparthenos nubilis*, *Euphydryas phaeton*, *Eutrapela clemataria*, *Feniseca tarquinius*, *Glaucopsyche lygdamus*, *Gluphisia septentrionis*, *Hemaris diffinis* (2), *Hemileuca grotei*, *Heterocampa guttivitta*, *Himella intractata*, *Horisme intestinata*, *Hydriomena transfigurata*?, *Hyles lineata*, *Hypercompe scribonia* (2), *Idia aemula*, *Idia lubricalis*, *Iridopsis larvaria*, *Lacosoma chiridota*, *Lochmaeus manteo*, *Macrurocampa marthesia*, *Nymphalis antiopa*, *Ochropleura implecta*, *Odontosia elegans*, *Orthosia hibisci*, *Palthis asopialis*, *Papilio troilus* (3), *Parasa indetermina*, *Patalene olyzonaria*, *Plusia putnami*, *Probole alienaria*, *Prochoerodes lineola*, *Psaphida styracis*, *Pyrrharctia isabella*, *Raphia frater*, *Schinia rivulosa*, *Scopula limboundata*, *Sphecodina abbottii* (2), *Spilosoma congrua*, *Spilosoma virginica* (4), *Symmerista canicosta*, *Synchlora aerata* (2), *Zale lunata*; PAUL GOLDSTEIN: *Eacles imperialis*; STUART GREEN: *Imbrasia belina*; ERIC HOSSLER: *Acronicta interrupta*, *Acronicta ovata*, *Acronicta spinigera*, *Acronicta superans*, *Allotria elonympha* (2), *Baileya ophthalmica*, *Cisseps fulvicollis*, *Citheronia sepulcralis* (2), *Clemensia albata*, *Crocigrapha normani*, *Cyclophora pendulinaria*, *Egira alternans*, *Elaphria versicolor*, *Ennomos subsignaria*, *Erannis tiliaria*, *Eulithis diversilineata*, *Glena plumosaria*, *Hemileuca lucina*, *Heteropacha rileyana*, *Hydrelia inornata*, *Hypoprepia miniata*, *Itame pustularia*, *Lapara coniferarum*, *Megalopyge crispata*, *Misogada unicolor*, *Morrisonia confusa*, *Nadata gibbosa*, *Nephelodes minians*, *Nepytia* nr. *pellucidaria*, *Panthea acronyctoides*, *Phosphila miselioides*, *Protitame virginalis*, *Rheumaptera prunivorata* (2), *Selenia kentaria*, *Simyra henrici*, *Smerinthus jamaicensis*, *Spodoptera ornithogalli*, *Timandra amaturaria*, *Tortricidia testacea*, *Zale helata* (2); CHARLENE HOULE: *Datana intergerrima*; JENNIFER JACOBS: *Dasylophia thyatiroides*, *Morrisonia latex*; DAN JANZEN: *Cocytius antaeus*, *Macrosoma conifera*, *Xylophanes pluto;* JULIA JOSEPH: *Paleacrita vernata*, *Panthea furcilla*, *Pleuroprucha insulsaria*, *Pseudothyatira cymatophoroides*; JEAN-FRANCOIS LANDRY: *Itame sulphurea*; MARC MINNO: *Atlides halesus*, *Fixsenia favonius*; RIC PEIGLER: *Sphingicampa bisecta*; NOBLE PROCTOR: *Melanchra picta*; JADRANKA ROTA: *Brenthia monolychna*, *Erynnis juvenalis*; JANE RUFFIN: *Parasa indetermina*; PAUL SCHAEFER: *Leucoma salicis*; LEROY SIMON: *Acronicta rubricoma*, *Battus polydamas*, *Calpodes ethlius*, *Danaus gilippus*, *Erinnyis alope*, *Eumorpha fasciata* (2), *Manduca rustica*, *Rothschildia lebeau forbesi*, *Siproeta stelenes*, *Xylophanes tersa* (2); MIKE THOMAS: *Peridea angulosa*; JAMES TUTTLE: *Hemaris gracilis*; RENE TWARKINS: *Comadia redtenbacheri*; MARTHA WEISS: shelter forming in *Epargyreus clarus* (insets); DAVID WRIGHT: *Satyrium edwardsii.*

INTRODUCTION

Caterpillars, the larvae of butterflies and moths (order Lepidoptera), are the last group of large, common, backyard creatures for which there are no comprehensive field guides. Every week of the growing season I am asked to identify caterpillars and answer questions about them: What is this? What does it eat? Is it a pest? Is it harming my house or garden? What will it turn into? How might I raise it? This guide will help you answer these questions for nearly all of the caterpillars likely to be encountered east of the Mississippi. Full species accounts with an image of the adult insect are given for 383 butterflies and moths; an additional 208 species are illustrated, but only briefly discussed (no adult images are provided); and 100 species are diagnosed, but not figured either as a caterpillar or adult. Included among these are forest pests, common garden guests, economically important species, especially handsome caterpillars, and others known to draw public interest. Of course, the Mescal Worm and Mexican Jumping Bean caterpillars are here. Of the 591 species for which a photograph has been provided, 114 are butterflies, far more than their relative diversity or frequency of encounter would justify, but because of their popularity with gardeners, children, and other naturalists, their numbers are well represented here. The species accounts are salted with additional images that illustrate earlier instars, closely related species, common parasitoids, interesting behaviors, and other aspects of caterpillar biology. While the area of emphasis is the East, this guide should be useful across the whole of southern Canada, portions of the Pacific Northwest, and at the generic level for most of the United States.

The North American diversity of Lepidoptera is immense. Close to 13,000 moth and butterfly species have been reported north of the Mexican border (Hodges *et al*. 1983, Poole 1996). Some 5,000 of these occur east of the Mississippi. Approximately 55% are "microlepidopterans," i.e., smaller moths, many of which are concealed feeders, fashioning and feeding within leaf shelters or boring into stems, fruits, and seeds. It is their counterparts, the "macrolepidopterans," that are the focus of this work. Most macrolepidopterans are exposed or "external" feeders that have distinctive forms, coloration, and patterning that readily allow for their identification. In some ways it is remarkable that a comprehensive field guide to such organisms has not appeared before now.

Caterpillars are enormously important in terrestrial food webs. They are the preferred grub, so to speak, for the nestlings of most of our songbirds. One piggish American Robin is reported to have devoured twice its own body mass in larvae over a 24-hour period. Spring would be silent in a forest without caterpillars. Caterpillars yield moths, which are important prey items in the diets of bats, martins, flycatchers, goatsuckers, and other vertebrates. Many caterpillars are important macrodecomposers, shredding fallen leaves, tunneling into dead wood, and consuming fallen fruits, thereby accelerating nutrient cycling processes. The silk in our sheets, parachutes, ties, lingerie, scarves, and other clothing comes from the Silkworm (*Bombyx mori*) and related moths. Adult moths and butterflies are important pollinators. Many of our most fragrant flowers, e.g., gardenia, narcissus, and jasmine, are moth-pollinated species. Hornworms or hawk moths are thought to be primary pollinators for about 10% of the tree species in tropical forests. Deserts also have many moth-pollinated plants. Indigenous peoples from every continent include caterpillars in their diets. Mopane caterpillars (*Imbrasia belina*, Family Saturniidae) are harvested and eaten by the millions in Botswana, Zimbabwe, and elsewhere in southern Africa (inset). Silkworm (*Bombyx mori*) pupae are regarded as a delicacy in China.

Mopane worm (Imbrasia belina) *harvest in Botswana.*

Caterpillars play a major, although indirect, role in all of our lives by exerting a chronic force on plants to evolve mechanisms to discourage herbivores. Plants are immobile. Caterpillars are omnipresent. If a plant is to survive through evolutionary time, it must have defenses, many of which are chemical: latexes, alkaloids, terpenes, tannins, and myriad others. Many of these compounds have medicinal (opium, salicylic acid = aspirin, digitalis, and taxol), culinary (tea, coffee, pepper, cinnamon, paprika, cumin, and other spices), and commercial (rubber and turpentine) values. And should you have an appreciation for fine red wines, be assured that the tannins that give the wine its body and character are there for an entirely different reason. Tannins are digestibility reducers manufactured by many woody plants that cross-link proteins and make them chemically unavailable to the organisms that ingest them. Thus, if only in a roundabout way, life would be considerably less rich and less interesting (and much less flavorful) without caterpillars.

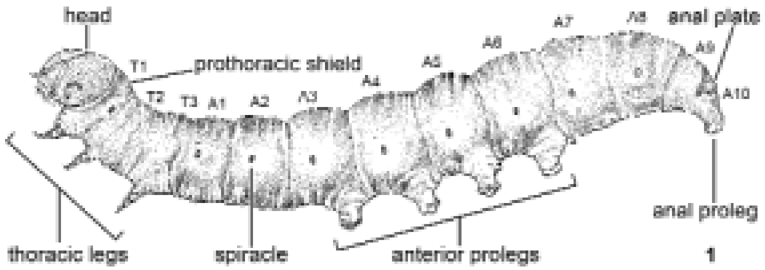


FIG. 1 *Lateral view caterpillar. T1 is the first thoracic segment, T2 the second thoracic segment, A1 the first abdominal segment, and so on.*

MORPHOLOGY

An insect's body is divided into three parts: head, thorax, and abdomen (Fig. 1). A diagnostic feature shared by all true caterpillars is an inverted Y-shaped line that extends down from the top of the head (Fig. 2). The lower arms delimit the **frontal triangle** or **frons**. Below the frons is a narrow plate, the **clypeus**, which runs between the two short **antennae**. The **labrum** or upper lip is positioned below the clypeus—its medial notch engages the leaf edge while the caterpillar is feeding. The caterpillar's six **lateral eyes** or **stemmata** are arranged, more or less, in a semicircle, with the fifth stemma usually offset toward the antenna. Located centrally on the lower side of the head is the labial **spinneret** (inset), the elongate spigot through which a caterpillar's silk is discharged. (Silk issues from the body as a liquid but turns to a solid fiber upon exposure to air.)

Frontal view of Brenthia monolychna *(Family Choreutidae). The spinneret of this microlepidopteran is especially well developed.*

The caterpillar's three thoracic segments bear true **legs**, each of which terminates in a simple claw. Extending across the top of the first thoracic segment (T1) is a variously developed

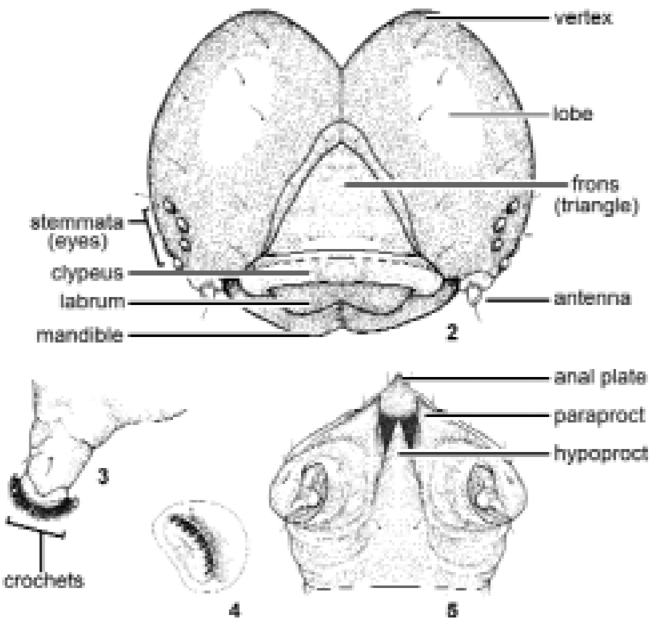


FIG. 2 *Head, frontal view.* FIG. 3 *Proleg, lateral view.*
FIG. 4 *Proleg with crochets, ventral view.*
FIG. 5 *Last abdominal segments of looper (Family Geometridae), ventral view.*

dorsal plate called the **prothoracic shield** (Fig. 1). Most of a caterpillar's mass is in its ten abdominal segments (A1–A10). **Prolegs**, the familiar, soft, hook-bearing legs of the abdomen, arise from the underside of abdominal segments three to six (A3–A6) and ten (A10) (Fig. 1). The number and relative sizes of the prolegs are often a clue to a caterpillar's identity. The prolegs bear a series of minute hooklets, called **crochets** (Figs 3, 4), that are used by the caterpillar to hold on to the substrate. Crochets, both their number and arrangement, are routinely used in keys by lepidopterists, although their use in this guide has been downplayed because they are difficult to view in living caterpillars. Structures of the last abdominal segment (A10) are often helpful in identification. The top of the segment bears a gumdrop-shaped **anal plate** (Fig. 1), which is sometimes pointed or otherwise modified. In inchworms the anus on A10 is flanked by the **paraprocts** and subtended by the **hypoproct** (Fig. 5).

Useful landmarks for orientation on the caterpillar's body include the spiracles and prolegs. **Spiracles**, the respiratory pores on the side of the caterpillar's body, are located on the first thoracic segment (T1) and the first eight abdominal segments (A1–A8) (Fig. 1). The spiracles on T1 and A8 are often twice the size of those that intervene. The midabdominal prolegs, as noted above, usually start on A3 and run to A6. In those moths with a reduced complement of prolegs, it is usually the anterior pairs that are reduced in size or absent.

For consistency, I use the term **stripe** for those markings that run parallel to the body axis and extend along a number of segments. An approximate terminology has been adopted to convey where the stripes are located: moving from the top of the body (dorsum) to the bottom (venter) are the **middorsal**, **addorsal**, **subdorsal**, **supraspiracular**, **spiracular**, **subspiracular**,

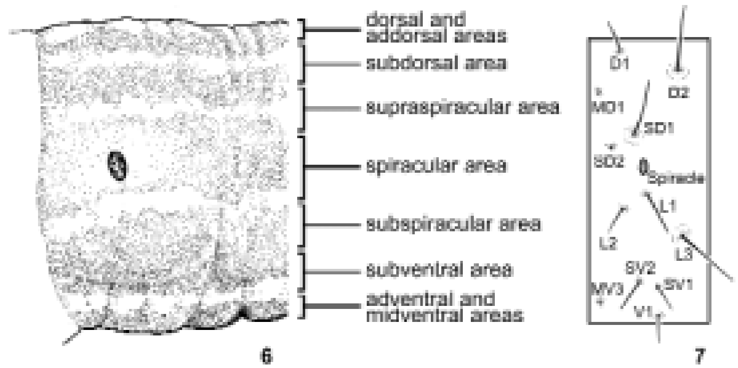


FIG. 6 *Abdominal segment, lateral view.*
FIG. 7 *Diagram of (primary) setal positions on idealized abdominal segment (head to left): D = dorsal, MD = microdorsal, SD = subdorsal, L = lateral, SV = subventral, and V = ventral. Hence there are two dorsal setae, 1 and 2, with D1 being more dorsal and more anterior than D2. Microdorsal setae are minute and require microscopic examination.*

subventral, adventral, and **midventral** stripes (Fig. 6). I use these terms to define relative position on a hypothetical cylinder (and ignore for the purposes of this guide technical arguments of homology that might be based, for example, on studies of larval development). Markings that wrap around the caterpillar's body are called **bands** or **rings**. The generic term **line** is used for shorter markings regardless of their orientation.

The size, arrangement, and number of setae on the head and body, or "**chaetotaxy**," have considerable significance in lepidopteran classification and identification. In this work I have largely avoided using chaetotaxy because most setae are difficult to see without the aid of a dissecting microscope. Nevertheless, there are several situations in the guide where specific setae are mentioned to assure a definitive identification. Setal nomenclature is easily learned—all the names are derived from a seta's position on the body (Fig. 7).

A glossary with numerous biological, morphological, and other specialized terms is provided at the end of this guide.

TELLING MACROS FROM MICROS

This book, with the exception of the slug caterpillars, smoky moths, flannel moths, and a few others, is focused on macrolepidopteran caterpillars. Macrolepidopterans are believed to represent a monophyletic group of "higher" Lepidoptera, most which feed exposed or externally on plants. Exceptions abound: some bore, a few form shelters, others are subterranean, etc. Many macrolepidopteran families have the crochets arranged in a line that runs parallel to the body axis. The majority of species of Lepidoptera and the overwhelming majority of individuals that you will encounter in nature are microlepidopterans (micros). Microlepidopterans are so diverse and heterogeneous as to defy ready characterization—most lepidopterists learn to recognize micros family by family until they garner a gestalt for their great variety. The lion's share of micros feed internally in leaf shelters, mines, galls, or tunnel into tissues. They tend to be rather simplified; warts, knobs, abundant secondary setae, spines, and other ornamentation are only occasionally evident. A significant portion of the common families has a well-differentiated prothoracic shield and rather plain thoracic and abdominal coloration. Microlepidopteran prolegs are often proportionately more slender and elongated. Their crochets are often arranged in a circle. One way to distinguish the two is to poke the caterpillar in question—if it wriggles backward with great rapidity it is certainly a micro (although if it does not wriggle backward, it can still be a micro since there are many micro families that do not respond in this way). This trick is especially helpful when you run across young macros that are too small to examine without a microscope.

NOT QUITE CATERPILLARS

The immature stages of wasps (especially sawflies) and some flies resemble caterpillars. Sawfly larvae are easily recognized by examining their heads or proleg complement. They have a single lateral eye (not six as in most Lepidoptera) and they lack a prominent protuberant labial **spinneret**. Most true caterpillars have four pairs of midabdominal prolegs (on A3–A6) or fewer; sawflies have five or more pairs (these usually beginning on A2). The prolegs of butterflies and moths bear numerous crochets; crochets are absent in sawflies, fly maggots, beetle larvae, and other caterpillarlike insects with fleshy abdominal legs. Some flower fly (family Syrphidae) larvae resemble caterpillars, but they lack a head capsule and always bear a pair of closely set spiracles at the rear of the body. Beetle larvae have from zero to six lateral eyes and lack a labial spinneret but are not likely to be confused with any of the caterpillars in this guide.

CATERPILLAR LOOK-ALIKES.
UPPER LEFT: Elm Sawfly (Cimbex americana) *on willow;*
UPPER RIGHT: Macremphytus *sawfly on dogwood;*
LOWER LEFT: Croesus latitarsis *sawfly on birch;*
LOWER RIGHT: syrphid or flower fly larva on beech (head to left).

CATERPILLAR LIFE CYCLE

All Lepidoptera have complete metamorphosis with four distinct life forms: the egg, **larva** or caterpillar, **pupa** or **chrysalis**, and adult. The egg stage typically lasts around 6–14 days, but it can be considerably longer in those species that pass the winter in this stage or for eggs laid in early spring when the temperatures may remain cool for weeks. The larval stage is the growth phase—some Lepidoptera increase their mass by more than 1,000 times as a caterpillar. To accommodate this growth, a caterpillar must molt, shedding its **cuticle** (integument or skin). The larva between molts is called an **instar**. Thus the first instar **ecloses** from the egg, the last or **ultimate** instar fashions the cocoon or cell in which pupation will take place, or, in the case of butterflies and some moths, spins the button of silk to which the chrysalis will attach. The majority of Lepidoptera have five or six instars. In some, like the Gypsy Moth (*Lymantria dispar*), the female caterpillar passes through an additional instar. Slug caterpillars (Limacodidae) go through as many as eight or nine instars. First instars may be dispersive, "ballooning" with the wind on strands of silk as do some of our inchworms and tussock moths or simply wandering great distances as do many catocaline noctuids (e.g., underwings). Prior to each molt the larva ceases feeding and becomes inactive—the next instar's head capsule may be observed within the prothorax of the quiescent, pre-molt larva. After the caterpillar sheds its old integument, it may take several hours before its new cuticle is hardened and it is again ready to feed. When the exact number of an instar is not known, it is often convenient to refer to these with terms such as middle, antepenultimate (second to last), penultimate (next to last), and/or ultimate instars.

The pupa, though sedentary, is a stage of great internal turmoil and transformation. Nearly all the larval tissues and organs—the eyes, mouthparts, legs, silk glands, muscles, etc.—will be digested and reorganized into the body of the adult insect. Prior to pupation the larva loses much of its patterning and its length decreases. In addition, the gut is evacuated. To the unaware, these caterpillars may appear diseased and close to death. Most moths pupate in a cocoon or cell fashioned in litter or soil. The naked pupa of true butterflies and a few moths is called a chrysalis; it tends to be sculptured, patterned, and may have a girdle of silk about the body near the juncture of the thorax and abdomen. In many species, the pupal stage lasts only 7–14 days while in others it may last many months, or in rare cases, two or more years. In those species that have facultative (partial) or staggered emergence, it is usually the pupal stage that holds in a state of suspended animation from one season to the next. But the record-holders here are the prepupal larvae of Bogus Yucca Moths (*Prodoxus*) of the American Southwest, which may remain viable and emerge as adults more than 30 years after they have ceased feeding!

Some species cycle through an entire generation in as few as four to five weeks—the Monarch being a familiar example. The longest life cycle belongs to the Arctic Woolly-bear (*Gynaephora groenlandica*), which routinely takes 14 years to complete its development. In Connecticut I would guess that our fauna is more or less divided between those species that have only one generation per year and those that have two; a small fraction have more than two broods and a handful take two full years to mature. Second, third, and additional broods are often facultative, meaning that some individuals in the population continue to emerge and reproduce while others enter **diapause** after a generation or two. (Diapause is a state of suspended development that normally coincides with a environmentally stressful period such as winter or the hot, dry portions of summer.) Members of facultative generations either continue to cycle through until the autumn brood(s) enter diapause or perish in inclement weather. Southward, most species add generations or broods. In southern Florida and Texas many moths and butterflies cycle through generations year-round.

Adults emerge from the pupa with short wings that must be expanded with **hemolymph**. Newly emerged adults, especially those with large, heavy wings, must be able to hang from a twig or other object to successfully enlarge their wings. The transformation from a hardly recognizable creature to a flight-ready adult is rapid, occurring, in some cases, over a span of only 20–60 minutes. It is one of nature's most captivating and awe-inspiring phenomena. At the age of six, I stumbled across a Buckeye Butterfly (*Junonia coenia*) emerging from its chrysalis. I did not know what I had found and was at the same time horrified and intrigued. Backing away, I watched from a safe distance. Within a span of five minutes, the Buckeye's hindwing spots were recognizable and, perhaps too, my path to become an entomologist had been largely fated. If you are rearing caterpillars, make sure you add to each container a twig or surface that your nascent adults may ascend and from which they can hang while pumping up their wings. Forewarning: wings with deformities and wrinkles after about 30 minutes are going to stay that way.

FINDING CATERPILLARS

There is no substitute for walking slowly and searching leaves, branches, and flowers individually. Only in this way will you learn about the insect's normal resting position, feeding behavior, threat displays, and other behaviors. Occasionally you might even observe interactions between a caterpillar and one of its natural enemies or see what stimuli evoke defensive or escape behaviors. The great majority will be found perched on leaf undersides, usually over a vein. Inspect leaf shelters. Leaves near the shoot apex are the most productive. I especially enjoy going out at night and searching by flashlight—most caterpillars feed principally at night. (In fact, one way to accelerate larval development times is to rear caterpillars in total darkness.) Nighttime searches are especially productive for those species that hide in crevices, perch along the trunk, or descend into ground vegetation at the base of their foodplant by day.

The most efficient way to secure caterpillars is with a beating sheet, which is just entomological for "drop cloth." The collapsible beating sheets sold by entomological supply houses are excellent, easily disassembled, durable, and dry quickly. White bedsheets also can be used to good measure—use them as drop cloths below vegetation that looks promising. Sheets are especially easy and efficient to employ when you are working with others (e.g., students).

Position a beating tray, sheet, umbrella, etc., under a limb of a shrub or tree and swiftly rap a branch, with the intent of knocking caterpillars from their perch, or grab a stem near its base, position the foliage over your sheet, and then strike the stem at any point above your hand. Usually a single swift rap or two is all that is necessary to dislodge the caterpillars. Do not jar the branch prior to striking it; the idea is to catch the caterpillars unaware. Many caterpillars have the ability to hang onto foliage tenaciously should they perceive the need to, e.g., during periods of high winds. After striking a few branches inspect the sheet for caterpillars. After a preliminary search, tip the beating sheet and gently pour away loose leaves and twigs. Then look to see if any caterpillars remain attached to the beating sheet fabric. The clearing of loose debris is especially helpful when looking for early instars that would otherwise be missed. For this reason, you may want to seek out a smooth white fabric for your beating sheet. Return unwanted caterpillars to appropriate foliage. While beating is effective anytime of day, early evening is especially good as many caterpillars come out of hiding to feed at dusk.

When using a beating sheet, sample only a single plant species; otherwise, your foodplant records will be in doubt, and you will be in a quandary about what to feed your caterpillars. Accordingly, make sure to completely clear your beating sheets between plant species so you can be sure that your foodplant association records are correct. (Note: caterpillars often crawl onto or come to rest on non-host foliage, especially larvae that are diseased, parasitized, or prepupal. Confirm feeding damage and/or the production of excreta before recording a species as a foodplant.)

Caterpillars that feed on grasses, forbs, or other low vegetation may be sampled by sweeping. Pass your net swiftly across target vegetation (a dozen times or so) and then check its contents for caterpillars. If there is considerable debris in the net, it often helps to dump the contents out over a beating sheet. Again, dusk and early evening efforts are generally more productive, and this is often the only way to find those species that shelter beneath, on, or near the ground by day. Wear a headlamp so that both hands will be free. Biological supply companies sell specially designed sweeping nets—these have a stout rim and a muslin net bag. Sweep only one plant species at a time and return unwanted caterpillars to their proper foodplant.

Burlap bands fastened around a tree trunk are a useful way to survey for caterpillars that leave the foliage and descend along the stem during the day to seek shelter. Burlap banding is one of the principal methods employed by forest managers to census Gypsy Moth caterpillar populations. Wrap a strip of burlap 15–20cm in width around a trunk at chest height, then use a staple gun to attach the band along its top edge. Cut three or four incisions upwards into the burlap, stopping a couple centimeters short of the upper edge so that flaps of the burlap can be lifted up while you search for caterpillars.

WHERE TO SEARCH

I enjoy the hunt, especially after I have been reading up on a species' biology and have planned a trip. As often as not, I fail to find what I am looking for, but invariably stumble upon other caterpillars just as interesting. To find caterpillars, watch for one of the many telltale signs that signal a caterpillar is present. Inspect leaf edges where you suspect recent feeding. If there is any hint of browning, the damage is old and likely you are too late for the quarry. The type of feeding damage may immediately reveal the identity of a caterpillar—larentiine geometrids and young hornworms chew characteristic holes in the middle of the leaf blade rather than starting from a leaf edge. Hornworms and underwing caterpillars often sever the petiole of leaves upon which they have fed. Fresh feculae (droppings) provide another sign that can narrow the search. The large feculae of hornworms and giant silkworms are especially obvious. If you are feeling especially motivated, throw a drop sheet down below a foodplant of interest—within hours, telltale feculae will be present to guide your search. Caterpillars that bore into plant tissues typically push frass out the entrance of their tunnel; such debris is a quick giveaway once you learn what to look for. My assistant, Eric Hossler, once found a Slender Sphinx (*Hemaris gracilis*) caterpillar by watching a parasitic wasp that seemed to be especially interested in a particular patch of lowbush blueberry. Some species use silk to form shelters, or crawl into those fashioned previously by other caterpillars. At first your efforts will be trial and error, but usually after two or three caterpillars are located, you will start to understand the biology of the species, finding caterpillars only on leaves of a certain age, perched in a characteristic position, sitting over the midrib on the underside of the blade, positioned in a cavity hollowed out along one leaf edge, etc.

Woodland and forest edges can be productive, particularly relative to forest interiors. While some species prefer saplings or shoots with new foliage, others shun such and restrict their feeding to mature foliage. Slug caterpillars are common on branches and leaves near the ground, whereas other species occur at chest height or in the canopy. I always check somewhat isolated plants, in preference to searching in large stands, where hundreds of leaves might be examined before a caterpillar is found. Gardens, plantings, and other plants in your own yard will yield gems. Vacant lots and highly disturbed habitats are home to species rarely encountered elsewhere.

WARNING

If you are collecting caterpillars with children it is a good idea to use caution when handling both hairy and spiny caterpillars. Even the Woolly Bear and the Hickory Tussock are allergenic to some people, or prove problematic if dislodged setae come into contact with the eyes, mucosal membranes, or other sensitive skin. While these and other noxious species (*see* pages 35, 53, and 238) may be picked up with the fingertips if handled gently and with respect, it is not recommended, especially around children.

WHEN TO SEARCH

The annual peak in caterpillar diversity is late spring, when there is an abundance of new foliage that often is not yet fully protected, chemically or physically. Some caterpillars feed only on older summer foliage. Flower and seed specialists tend to come along later in the season. Those that feed on fallen leaves or tunnel in wood seem to be equally common year-round. For many of the larger species it is hard to beat late August and September, especially if you like searching for my three favorite groups, the daggers, prominents, and slug caterpillars. Flashlight searches at night are invariably productive at this time of year.

Timing is everything. The peak of activity for a species may be brief, spanning only two to three weeks. A species that seems impossibly scarce one week might be common the following, then just as quickly disappear for the remainder of the year. Of course, you can broaden the window of opportunity for your efforts by developing a search image for earlier instars (smaller larvae) or even eggs. Species with two or more generations provide second and third chances. Mountainous regions such as the Appalachians provide a special opportunity—a general rule of thumb is that every 300m (1,000ft) of altitude corresponds to a week or so in seasonal phenology. Thus a species that is mostly pupal at 150m (500ft), may be present as mature larvae at 450m (1,500ft), and as penultimate instars at 750m (2,500ft).

REARING CATERPILLARS

I would venture that a fair fraction of professional entomologists and especially moth enthusiasts were drawn into entomology in part by the rearing of giant silkworms and other interesting caterpillars. Caterpillars are little mysteries, much of the time you are not sure how they will turn out. I always enjoy checking my rearing room for the recent emergences so that I might associate an adult with what, up until that instant, had been an unidentified caterpillar.

While some will want to rear caterpillars simply because they enjoy watching metamorphosis or find it is an activity that they can share with their children or students, there are a number reasons why the serious student of entomology will want to delve into the business of rearing immature stages. It is one of the most efficient methods for obtaining series of some species, especially leafminers, gall makers, and other microlepidopterans. Immaculate individuals may be obtained for photography and released or vouchered and donated to a museum—reared specimens with full foodplant data are valuable study specimens, particularly if they prove to be part of a taxonomically difficult species complex. Carefully observed rearing lots will yield a wealth of information on feeding habits, periods of activity, development times, and other life history information. As noted elsewhere, rearing of wild-collected caterpillars is the principal means to document a species' parasitoid and pathogen fauna.

There is nothing magical about rearing: if one supplies fresh foliage, keeps the rearing containers free of mold, and provides benign temperature and moisture regimes, the successes will be many. I rear most of my singleton caterpillars in 15 dram and 40 dram plastic vials. Larger collections are held in pint or quart take-out containers. I employ large plastic pretzel jars and one-gallon ice cream cartons on occasion. Into the latter, I cut windows and cover these with fine netting fabric. Several colleagues recommend sandwich boxes, in part, because they are very easy to clean. An especially attractive aspect of the take-out containers noted above is that the basket-type disposable coffee filters sit perfectly within and function like napkins, allowing the rearing containers to be cleaned quickly and with little fuss.

While closed containers are acceptable to many species, others require ventilation—Luna Moths (*Actias luna*), Cecropias (*Hyalophora cecropia*), and Buck Moths (*Hemileuca maia*) succumb to a wilting disease when reared in saturated atmospheres. It is often helpful to punch small holes into the lids of your rearing containers. For special collections, use water picks or other measures to insure that the foliage stays fresh. Keep larval densities low as overcrowding will result in smaller adults, unnatural larval color morphs, and promote the outbreak and spread of disease.

Coffee filters or paper toweling placed over the bottom of the rearing containers will absorb excess moisture and allow the feculae (excreta or droppings) to be quickly removed. In the last instar, a 3–5cm layer of very lightly moistened peat is often a better option than toweling. In the wild many caterpillars tunnel into soil to fashion their pupal cell. A few of the spring-active owlets may tunnel as deep as 10cm or more to pupate. Peat has other advantages: it soaks up excess moisture, releases moisture over a period of weeks, and serves as a mold retardant. Some caterpillars (e.g., daggers, brothers, and forester moths) fashion pupal chambers in soft wood and will die if they cannot find a suitable pupation medium. Chunks of styrofoam or pith may also be employed.

Provide appropriate foodplant material—some caterpillars will eat only new leaves, while others are obligate old-leaf specialists. Flower moths (*Schinia*), cucullias, and many blues prefer flowers. Others consume only seeds and fruit. This book will help you sort through the possibilities, but you can make reasonable guesses. For example, spring-active species with a single generation are almost certainly new-leaf specialists; fall-active caterpillars with bright colors are good candidates for flower-feeders; ground-foraging caterpillars will often accept a variety of forbs. When in doubt, provide a salad of choices, and then watch for the production of feculae and check for feeding damage. Oak is eaten by more species than any other plant in this guide. Other foodplants that are suitable to large numbers of forest caterpillars include alder, apple, birch, cherry, poplar, and willow. Some caterpillars will accept substitutions; it is often convenient to offer common foodplants from your yard or choose a plant species whose foliage stays fresh over longer periods. Forbs acceptable to a number of moth caterpillars that forage on low-growing plants include clover, dandelion, dock, fleabane, and lettuce. The latter can be purchased year-round. Because of its high water content, it is best to use the greenest portions of the outer leaves or purchase Romaine and other leafy varieties. Many boring (tunneling) moths, e.g., Goat Moths (Cossidae), Ghost Moths (Hepialidae), *Papaipema* (Noctuidae), may be reared on carrots. If you have a coring tool, carve out an initial tunnel, scarcely wider than the caterpillar's own diameter, into which you can introduce your larva (Richard Henderson pers. comm.).

Caterpillars should be minimally disturbed prior to molting and pupation. Pre-molt larvae can be recognized by their quiescent behavior and proportionately small head. Feculae production drops off prior to each molt. Many species spin a light sheet of silk into which they engage their crochets, thus anchoring the caterpillar so that it may, literally, crawl out of its old skin. The head of the ensuing instar is usually visible as a swollen lump within the first thoracic segment and the black lateral eyes of the next instar can be seen through the integument of the soon-to-be-shed skin (*see* page 407, Shivering Pinion, *Lithophane querquera*). Pre-molt larvae are vulnerable and have limited mobility; care should be taken not to dislodge them from their purchase. Prepupal larvae often enter an extended wandering

phase, appear somewhat shorter and plumper, show no interest in food, are dull in coloration, or lose their patterning.

For large rearing efforts, consider sleeving your caterpillars (inset). Your principal concerns will be to ensure that there is sufficient foliage of the appropriate age for the caterpillars in the sleeve and to remove prepupal caterpillars that might tunnel through the sides of the netting in their search for a suitable pupation site. In addition to being comparatively low maintenance, sleeving has the advantages of yielding full-sized adults whose development is synchronized with that of wild caterpillars. Additionally, disease outbreaks are exceedingly unlikely. The one- and five-gallon paint filter bags sold at larger hardware stores are fine-meshed and make excellent and economical sleeves. Insect net bags may be used as well, but they are expensive. Pillow cases will serve as sleeves and are very economical, especially if purchased used or on sale. Entomological supply houses sell sleeves that tie off at both ends and have a side zipper for easy access and servicing. We make our larger sleeves out of tenting fabrics (available over the Internet). Double-sleeve especially valuable caterpillar cohorts to provide greater distance between your livestock and potential predators. On numerous occasions I have observed predaceous stink bugs sitting on the outside of my sleeves, taking a meal from within. Birds may peck holes through the fabric to get at the occupants. Large sphinx and silkworm caterpillars are particularly apt to draw the attentions of birds. Always shake the branch vigorously before adding your caterpillars to the sleeve as spiders, assassin bugs, predaceous stink bugs, and other predators would like nothing better than to be sealed up with a clutch of caterpillars. Caterpillars placed on sunny branches generally do better. For species that feed on grass, forbs, and other small plants, transplant some foodplant into a pot and then sleeve an appropriate number of caterpillars within.

Insects are "cold-blooded," and thus their rate of development may be controlled by rearing them at different temperatures. Rearing indoors accelerates the development of spring-active species. Conversely, most caterpillars tolerate short stints of a week or more in a refrigerator if the temperatures are kept above freezing. As most caterpillars are principally nocturnal, it is often possible to accelerate the rate of development by rearing your caterpillars in complete darkness.

While it is laudable to release livestock into the wild, be steadfast in making certain that your releases are biologically and genetically appropriate. Never release insects from one province, state, or region into another. The potential for calamity is great: one could transfer pathogens and disease from one population to another or introduce inappropriate genes. At the very least, you will be scrambling the genetic history of two populations, corrupting any signal that might be studied by scientists in the future. Be circumspect about your decision to take a moth from that lighted gas station wall on your way through Alabama on your way back to Massachusetts—none of its progeny should be released in the Northeast. Additional suggestions for collecting and rearing caterpillars can be found in Covell (1984), Friedrich (1986), Dunn (1993), Winter (2000), Leverton (2001), and Wagner *et al*. (2002).

OVERWINTERING LARVAE AND PUPAE

The greatest rearing challenge is getting your livestock through the winter. It is not simply a matter of keeping everything alive—for most species you must break the obligatory diapause. In temperate insects, diapause is broken by a prolonged exposure to cold temperatures. But how cold and how long? I generally hold my collections for 12–16 weeks at temperatures just above freezing. The key variables over this period are moisture and temperature, with the former being hardest to control. Many batches will desiccate and others will mold if you are not vigilant. A stairway leading out of a basement with a protected bulkhead or hatchway makes for an ideal location. The lots will be exposed to natural humidities and should stay above freezing. Keep a thermometer or plastic container of water next to your collections so that you can periodically check that they are not exposed to freezing temperatures. Another option is to winter your collections in a shallow hole dug in the ground that is then covered with sticks or wood and buried under 10–25cm of leaves. The tops of the containers should be open so the livestock is exposed to fluctuating humidities. I cover my containers with squares of nylon netting (or even squares of fabric), invert them so they will not fill with water, and place them on plastic garden flats. The latter also serves to exclude mice that might feed on the collections through the winter. Old wood sheds, garages, and back porches are also good overwintering sites, but depending on conditions (and the geographic regions from which you have made your collections) you will need to shield them from subfreezing temperatures and/or may have to lightly moisten your lots occasionally, etc. Collections from the South may be freeze-intolerant, while those from Maine may endure long periods of subfreezing temperatures. Advice from Dale Schweitzer, with whom I often consult about all things lepidopterological, "A good general rule is that underground pupae should not be exposed to temperatures below 20–25° F. Unless your climate frequently has nights below about 10° F the easiest approach might be keeping above-ground pupae outside in a shaded sheltered place." Carter and Hargreaves (1986) recommend keeping pupae in a cold but frost-free site.

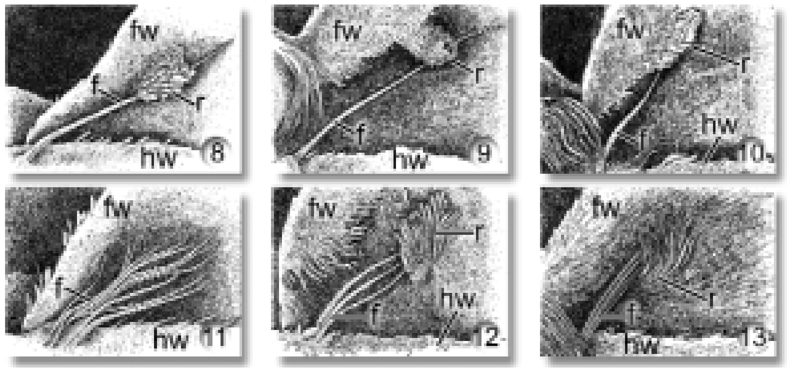
STARTING WITH EGGS

When your searches are focused on single species, it is often possible to sleuth out the eggs, the most numerically abundant life stage for any insect. Those moths that lay their eggs in masses, such as buck moths and tent caterpillars, present little challenge to see other than the fact that their egg masses may be widely spaced and infrequently encountered. The eggs of giant silkworms, hornworms, swallowtails, and prominents are large, spherical, usually smooth, and quite visible to the unaided eye. Smaller species present special, but far from impossible, challenges. The famous American entomologist Harrison Dyar urged those interested in finding slug caterpillars to look for the flat, glassy eggs, which he claimed are both numerous and easily located once one develops a search image for the shiny spots on leaf undersides (Dyar 1899: 241). Eggs laid in the summer may hatch within 4–10 days, although exceptions abound. Those moths and butterflies that hibernate as eggs may spend the better part of their lives in this stage. For example, tent caterpillars (*Malacosoma*) spend five times as long in the egg stage as all the other stages combined. Leverton's book *Enjoying Moths* (2001) has additional tips for finding eggs.

Another means of obtaining eggs is to confine a mated female for a night or two. Corrugated or scratched cardboard, a twisted piece of toweling or paper, or other roughened surfaces, may stimulate egg-laying. While most females lay in virtually any situation, others have specific requirements and will refuse to lay unless a sprig of the foodplant, a piece of bark, bud or flower, etc. is supplied. Conversely, female prominents, daggers, and slug caterpillars seem to prefer smooth-walled containers. Styrofoam coolers may be used for large moths—many times the wings will be unblemished even after a night or two of confinement. Sleeving females on an appropriate foodplant nearly always works. Some species must feed for a night or two before they will lay. Other species seem to yield eggs more freely if held in completely clean, smooth vials for a night without any food and water: I often do this on the first night that I hold a female or after two or three nights of feeding without obtaining eggs. Some degree of ventilation is sometimes needed.

Gravid females of most moths come to light, but the preponderance of individuals arriving at lights will be males. According to Richard Heitzman, just after dark can be especially productive for females. I have found foggy, wet nights good for females, at least relative to the total number of moths that arrive at light. Females of some giant silkworms (e.g., the Cecropia, *Hyalophora cecropia*) and others fly mostly after midnight, so it may be necessary to run your lights throughout the night. More balanced sex ratios can be expected at baits and flowers.

Incubate your eggs under natural humidities, and in dry weather mist them occasionally. Eggs are susceptible to mold so it is a good idea to check them at least once a day. Eggs held with foliage from the foodplant in closed vials will nearly always mold before hatching. Viable eggs are often pale cream when laid, add color over the first day, then darken, clear, or in some other way change color again a day or so before the first instars issue. Eggs that stay cream-colored and/or collapse are typically infertile. If your eggs take more than ten days to two weeks to hatch they are likely dead or destined to overwinter. Newly hatched first instars are vulnerable creatures that soon starve or desiccate if they do not have ready access to appropriate foliage. A fair number of newborn caterpillars consume part or all of their eggshell for their first meal. I often mist newly hatched larvae, especially if they have been wandering without foliage for any period of time. I take greatest care with first instars of slug caterpillars; I transfer these individually to the underside of an oak-leaf sprig held in a small water pick, mist them thoroughly, and then let the leaves air-dry for a half hour or so while the minute caterpillars establish.



WING COUPLING MECHANISMS IN MOTHS: MALES ABOVE AND FEMALES BELOW.
FIG. 8 *male of* Metarranthis obfirmaria *(Family Geometridae);*
FIG. 9 *male of* Haploa lecontei *(Family Arctiidae);*
FIG. 10 *male of* Lymantria dispar *(Family Lymantriidae);*
FIG. 11 *female of* Metarannthis obfirmaria*;*
FIG. 12 *female of* Haploa lecontei*;*
FIG. 13 *female of* Lymantria dispar.
fw = forewing, f = frenulum, hw = hindwing, r = retinaculum.

SEXING ADULTS

A reliable means to determine the sex of most moths is to examine the frenulum, the coupling spine(s) that extends up from the base of the hindwing and engages specialized scales on the underside of the forewing (Figs 8–13). It is single and thickened in males; it is double-, triple-, or multispined in females. It is helpful to hold the wings together, preferably with a pair of spade-tipped forceps or stamp tongs, over the moth's "back" to view the frenulum. If done carefully,

Male Sallow (Sunira bicolorago). *When sexing adults, look for a line or gap between the male's claspers.*

Male Sallow (Sunira bicolorago) *with valves partially spread as they might appear immediately before coupling (with female).*

this does not harm the moth. The male antennae are generally more plumose or set with more sensory setae (males use their sensory setae to detect female sex pheromones). Sexual differences in the antennae are abundantly obvious in giant silkworm moths and tussock moths; examination of the antennae, with or without the aid of a lens, will usually reveal sexual differences in other moths. Many male Lepidoptera have specialized scent scales on their legs, wings, or abdomen that immediately reveal their sex, but knowing where to look usually requires prior knowledge as these scales are often concealed. Females tend to be larger and their abdomens fuller and more rounded, especially rearward. In many owlets the male spermatophore can be felt within the female's abdomen by gently pressing the abdomen between thumb and forefinger. Male Lepidoptera have side to side claspers (or valves) that hold the female during mating—look for a slit along the venter where the valves come together (insets). Females have a circular pore, often with associated extrusible pads, which they use to taste the foodplant or deposit egg(s). By gently pushing on the end of the abdomen it is often possible to expose enough of the genitalia to know what sex you are holding, but this will take practice. Remember: when searching about lights, the great preponderance will be males.

FEEDING FEMALES

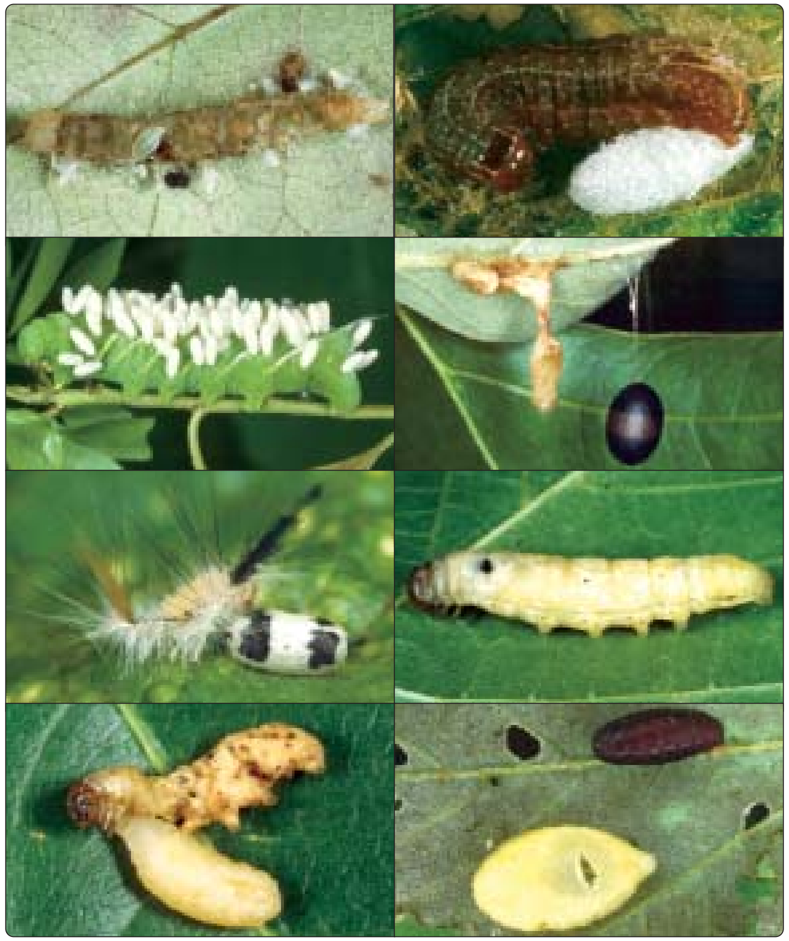
Some females need to be fed before they will lay eggs. A feeding solution of one part sugar, maple syrup, or honey to two parts' water, offered in a tiny ball of cotton, will suffice. Sometimes it will be necessary to uncoil the female's tongue with a pin and place its tip in contact with the solution. I usually leave a small (4–5mm) feeding ball with the female, changing it every day or two. Another option is to offer females a small chunk of a grape, soaked raisin, or apple slice. I use raisin slices, perhaps 1/5th of a raisin, that stick fast to the side or the top of a vial, especially when traveling. This will prevent the female from getting stuck on her back, which often results when food is placed on the bottom of the vial. Change the fruit after 3–4 days, before it begins to mold. Females held in sleeves can be fed by misting a part of the sleeve and foliage with a sugar-water solution (Tom Allen, pers. comm.) or leaving a cotton plug soaked with food on the outside of the sleeve in a position where the female(s) can get to it. Although the water in this solution soon evaporates, nighttime moisture may dissolve enough of the sugar for the females to feed; alternatively, the sleeve can be lightly moistened with water once or twice a day. Confine females during the appropriate season, e.g., female fritillaries (*Speyeria*) rarely lay before the latter half of August or even September. Moths that emerge in the fall often pass the winter unmated, and do not pair and lay until the following spring.

NATURAL ENEMIES

The number of enemies a caterpillar faces is legion. Every major group of terrestrial vertebrates has species that prey on caterpillars. Visual predators surely have shaped the varied coloration and texture of caterpillars, and even their feeding and resting behaviors. Birds in particular have been a major selective force in the evolution of caterpillar appearance and behavior. Stated differently, caterpillars are visually and behaviorally fascinating creatures largely because of avian predation. A distant second in importance are the insect-feeding vertebrates such as frogs, lizards, snakes, shrews, and mice. Even bears, foxes, and other large mammals hunt for and consume caterpillars.

Many groups of invertebrates are predators of caterpillars. Their importance in controlling caterpillar populations is best appreciated in agricultural systems where birds and other vertebrate animals are relatively scarce. Without predaceous beetles, mites, spiders, earwigs, stink bugs, lacewings, ants, wasps, and myriad other insects, caterpillar populations would quickly consume the world's croplands, orchards, and forests. In the tropics and some temperate communities ants are major predators. Hornets and wasps harvest large numbers of caterpillars—some farmers even provide nesting boxes for wasps as part of an integrated pest management regimen to lower their dependence on pesticides. Robert Muller, whose hobby of late has been the mass rearing and release of giant silkworm moths (Saturniidae), has observed the introduced paper wasp (*Polistes dominulus*) consuming many of the caterpillars that he set out in his yard in Milford, Connecticut to augment local populations of silkworms.

Parasitoids have an enormous influence on caterpillar populations. Parasitoids are specialized predators, smaller than their prey, that feed like a parasite on or within the body of their victim. They are distinguished from true parasites because they nearly always kill their host—they just do it slowly, over a period of days, weeks, or even months, and usually from within. A common parasitoid life history strategy is to develop slowly and feed on non-essential tissues and organs, but then vanquish the host caterpillar in a final burst of growth. In this way their food (the caterpillar host) does not spoil and is able to behave normally, e.g., avoid the attentions of a bird that might consume both the caterpillar and developing parasitoid in a single act of predation. Many parasitoids are specialized, attacking a single caterpillar species or group of related species. Several of the largest and most diverse evolutionary lineages on this planet include caterpillar parasitoids: tachinid flies (>20,000 spp.), braconid



COMMON CATERPILLAR PARASITOIDS.

TOP ROW LEFT: *Several* Euplectrus *(Family Eulophidae) wasp larvae issuing from cadaver of noctuid.*

TOP ROW RIGHT: Microgaster scopelosomae *(Family Braconidae) wasp cocoon beneath third instar Sallow* (Eupsilia) *larva.*

SECOND ROW LEFT: Cotesia congregata *(Family Braconidae) wasp cocoons on Pawpaw Sphinx* (Dolba hyloeus).

SECOND ROW RIGHT: Meteorus *(Family Braconidae) wasp cocoon suspended from silken thread.*

THIRD ROW LEFT: Hyposoter *(Family Ichneumonidae) wasp cocoon beneath corpse of White-marked Tussock Moth* (Orygia leucostigma).

THIRD ROW RIGHT: *Speckled Green Fruitworm* (Orthosia hibisci) *with single tachinid fly maggot within its body. The black spot is necrotic tissue associated with the maggot's breathing tube, which it has pushed through the wall of the caterpillar's body.*

BOTTOM ROW LEFT: *Same caterpillar with maggot freshly emerged from the Speckled Green Fruitworm caterpillar.*

BOTTOM ROW RIGHT: *Tachinid fly puparium above recently vanquished cadaver of Yellow-shouldered Slug* (Lithacodes fasciola). *Tachind fly maggots pupate in their last larval skin, forming a hardened puparium.*

wasps (>40,000 spp.), ichneumonid wasps (>60,000 spp.), chalcidoid wasps (>400,000 spp.), and numerous smaller superfamilies and families (numbers are estimated species diversity). By comparison, true parasites are few in number. They include a number of mites (*see* page 165) and minute ceratopogonid flies, both of which feed on host hemolymph or "blood" but seldom harm their host.

At first you may find it both frustrating and disappointing if your hard-sought caterpillars prove to be parasitized. But parasite records are of great value, especially if the host (caterpillar) is known with certainty. There is much concern about the effects of parasitoids that have been introduced into North America to control pest species. One egregious example is *Compsilura concinnata*, a tachinid fly that was introduced to control the Gypsy Moth (*see* pages 245 and 296). Its host range, which includes more than 200 native butterflies and moths, is incompletely known; little quantitative data exist for its rates of parasitism of our native butterfly and moth species.

Like other multicellular organisms, caterpillars are attacked by viruses, bacteria, fungi, and other pathogens. Pathogens are important in regulating population numbers, especially under outbreak conditions when populations are dense and disease can pass easily from one individual to the next. Gypsy Moth populations east of the Appalachians are often regulated by the fungal pathogen *Entomophaga maimaiga* and a nuclear polyhedroris virus. The bacterium *Bacillus thuringiensis* is used widely to control caterpillar numbers in turf, gardens, orchards, and forests. Various formulations of "Bt" may be purchased from nearly any greenhouse, nursery, or agricultural supply store. Maybe it goes without saying that if you see a caterpillar that appears diseased, it should be immediately isolated from others that you are rearing. Caterpillars that blacken and ooze unpleasant odors are often victims of bacterial infections.

Caterpillar populations are kept in check by the collective impacts of the natural enemy complex. The exact mix and relative importance of the predators, parasitoids, parasites, and pathogens in the enemy complex varies from year to year and site to site. Outbreak species are those that occasionally escape their enemies and build to numbers where they defoliate acres of forest. But even these, within days, weeks, or generations, are inevitably found and their numbers driven down, sometimes to the point of scarcity! It is a race for survival—a race that most caterpillars will lose. From the beginning the odds are against the caterpillar. Each week the ranks are thinned in large measure. To compensate for these losses, insects may be very fecund—one Australian moth produces upwards of 50,000 eggs per female. Considering these numbers, it becomes obvious why it is so advantageous for the serious enthusiast to search for earlier life stages, the most numerous of which are the eggs (*see* page 19).

SURVIVAL STRATEGIES

Caterpillars employ a fascinating battery of stratagems to escape the attentions of their enemies or to thwart the attacks that follow once they have been discovered. Prior to discovery the principal tactic is crypsis—blending into the background so as to avoid detection. Caterpillars are exceptionally adept at matching the leaves or needles upon which they perch and feed. A wonderful example is the Double-toothed Prominent (*Nerice bidentata*) (*see* page 289) whose coloration and outline approaches that of the elm leaves upon which it feeds. Many leaf-feeders exhibit "countershading," whereby the lower portion of the body becomes progressively lighter green so that the insect's own shadow scarcely changes the overall impact of the caterpillar's coloration when viewed from a distance. Caterpillars may resemble petioles, twigs, bark, buds, flowers, fruits, or tendrils. The inchworms are consummate background-matchers—while beating foliage I am forever having to squeeze this and that to make sure that a plant fragment is not, in fact, a caterpillar. Several emeralds, e.g., the Camouflaged Looper (*Synchlora aerata*) (*see* page 200), go so far as to attach flower bits and other pieces of vegetation over their bodies to better blend into their background. Among the most striking bark and stick mimics are those that have markings that resemble foliose lichens, e.g., the Ilia Underwing (*Catocala ilia*) (*see* page 363) and Kent's Geometer (*see* page 179). Some caterpillars look like the dead leaves of their foodplants—the majority of these, interestingly, also quaver back and forth if disturbed, much like a dried leaf might do in the wind. Among those that rest on bark, a large fraction possesses a prominent subventral line of hairs or setae. While generally termed "shadow elimination hairs," they seem to function principally in another capacity, i.e., to disguise the outline of the caterpillar and make it difficult to distinguish bark from caterpillar (*see also* page 365, White Underwing). A few are highly polymorphic with forms so different that a predator would need to learn many search images to recognize all the individuals present in a single shrub or tree (e.g., The Little Wife, *Catocala muliercula*, *see* page 364). Others employ disruptive coloration, whereby bold bands and other prominent markings break up the caterpillar's otherwise recognizable appearance, and diminish the probability that it will be recognized (e.g., Abbott's Sphinx, *Sphecodina abbottii*, *see* page 270). Many resemble bird droppings. Interestingly, these typically have shiny integuments and thus appear as fresh wet droppings, considerably more so than if their integument were not so rendered. A few of our caterpillars mimic other protected animals: among the models are snakes, the cast skins of tarantulas (*see* page 44), sawfly larvae, and unpalatable caterpillars.

Some blues and hairstreaks enlist the help of ants to guard them from predators and parasitoids. Not only have lycaenids evolved special appeasement and nectar organs to moderate these interactions, but many also have stridulatory (sound-producing) structures that are used to "call" ants into service. The caterpillars' calls are substrate-borne, carried through the foodplants and other surfaces, so that ants walking nearby can detect the vibrations with their feet.

Silk may be used to build shelters or nests that serve to conceal the caterpillar as well as exclude enemies. Numerous groups spin a belay line upon which they rapidly descend if disturbed; once danger has passed, some will ascend their silken tether and return to their foodplant. This behavior is taken one step further in some ennomine geometrids: in advance of any disturbance, they spin down on a short belay 2–5cm in length to pass the hours of darkness.

A common strategy is to drop from the foodplant. A mere wisp of air (or breath) may be sufficient to make a cutworm release its grip. Among the Geometridae and Noctuidae there are caterpillars that are more animated in their response, literally hurling themselves from their perch if startled or molested. Some have strongly muscular wriggling responses that may go on for seconds. The wriggling may be so violent as to cast the caterpillar to and fro, a behavior that often buries the insect in loose surface litter.

Many species attempt to bite or feign like they are going to do so. Although none of our species inflicts a bite of any consequence to a human, I must admit to being startled occasionally, especially if the action is rapid as in many underwing (*Catocala*) caterpillars. While far from universal, I have almost come to expect that roughly handled caterpillars will regurgitate—the fluids are sometimes quite sticky and unappealing and, no doubt, in some cases noxious. False heads and eyespots have evolved in many moth and butterfly lineages, typically at the rear of the body such as in the Gray-patched Prominent (*Dasylophia thyatiroides*) (*see* page 316) and Turbulent Phosphila (*Phosphila turbulenta*) (*see* page 427). In swallowtails false heads occur over the thorax. Regardless of where they are situated, the caterpillars that bear them have an associated behavioral defense: they bite, regurgitate, or deliver a defensive substance at the time the false head is pecked or probed. Two of our sphingids make audible noises when perturbed: Walnut Sphinx (*Amorpha juglandis*) (*see* page 264) caterpillars hiss by forcing air out their spiracles, while those of the Abbott's Sphinx (*Sphecodina abbottii*) (*see* page 270) much like a mouse when provoked.

Caterpillars may defend themselves physically and/or chemically. Many warn of their unpalatability with aposematic (warning) coloration: the usual is some combination of red, orange, and yellow with intercalated black and white markings for accent, although just the latter two also work for many. Warningly colored caterpillars often feed gregariously, which serves to reinforce the message that they are unpalatable. Hairs and spines provide physical protection. The former, which are frequently deciduous and not infrequently microscopically barbed (tiger moths and others), provide protection from many birds and other enemies. (Curiously, cuckoos have a predilection for hairy caterpillars and have exaggerated whiskers about the base of the beak presumably to protect the eyes from thrashing caterpillars.) Brushfoots are well known for their armor of many-branched, stout spines. Caterpillars from three families, the giant silkworm moths, flannel moths, and slug caterpillars have hollow, poison-filled spines that deliver potent stings, with some tropical relatives reported to cause human deaths! Some tussock moth caterpillars release a potpourri of noxious compounds from the reddened glands atop abdominal segments six and seven that can be quite irritating to humans, and especially to those that are hypersensitive. An especially well-protected species is the Brown-tail Moth (*Euproctis chrysorrhoea*), another tussock, which bears hundreds of deciduous spicules (modified setae) along the dorsum that cause severe dermatological reactions in humans, and on rare occasions, even death (*see* page 453).

Some caterpillars sequester toxic compounds or manufacture them from precursors obtained from their foodplants. Toxin concentrations in the caterpillar's hemolymph ("blood") may be many times those found in the leaves of their foodplant. Tiger moths are among the most well protected, sequestering or manufacturing biogenic amines (e.g., histamine), pyrrolizidine alkaloids, cardiac glycosides, and other noxious substances. Smoky moths manufacture cyanide-containing compounds. As a general rule, expect that brightly colored caterpillars are protected or that they are mimics of unpalatable species.

For every stratagem enumerated above there are many that are not mentioned—the literature on defensive strategies is both enormous and engaging. Behavioral adaptations that aid in survival are especially numerous and varied. Natural enemies not only influence when some caterpillars eat, but also how they eat, or even what they eat (because survivorship will be higher on some foodplants than others), or how they defecate. And while it is easy to associate a given butterfly or moth caterpillar with one of the above defenses, in fact, most species stack strategy upon strategy, ruse upon ruse, in order to win the battle between predator and prey. My favorite case in point is the Spicebush Swallowtail (*Papilio troilus*). For the first three instars it mimics a bird dropping, then it molts into a snake mimic that resides within the confines of a leaf shelter. As a last line of defense, it will deploy and flail about its osmeterium, an eversible tentaclelike structure that is laden with butyric acid, a substance that to me smells like fresh vomit. Jeff Boettner (pers. comm.) has twice observed a Spicebush ward off vespid wasp attacks with its osmeterium—not only were the attacks terminated but the wasps seemed to have been temporarily felled to the ground as a result of their exposure to the osmeterial secretions.

PRESERVING LARVAE

The serious student may want to preserve eggs, larvae of various instars, and pupae for later study. Such specimens become the basis for future taxonomic and ultrastructural studies. The easiest way to preserve larvae is to drop them into gently boiling water and then remove both water and caterpillars from the heat source. As soon as the caterpillars are fully distended, usually within seconds of having been placed in the boiling water, they can be transferred to 70% ethanol. Caterpillars killed simply by immersion in ethanol often discolor, sometimes turning black within minutes. A superior larval specimen may be obtained by injecting the body cavity with fixative using a fine needle (#30 for very small caterpillars and #27 for larger specimens). Slowly fill the body with fixative until the caterpillar and its prolegs are fully distended. A simple fixative that yields excellent specimens is made by combining nine parts 70% ethanol with one part acetic acid. Recipes for other cold preservation fluids, based on various combinations of alcohol, formaldehyde, and glacial acetic acid, such as KAAD and Kahle's Fluid, are discussed in Stehr (1987) and Winter (2000).

Because many caterpillars continue to leak particulate matter from both ends of the gut after they have been preserved, it is best to transfer the specimens into fresh 70% ethanol after a week or two, before any material sets up on the specimen. Keep in mind that while higher concentrations of ethanol are preferred for DNA preservation, these can dehydrate tissues and cause the caterpillar to collapse and lose its form.

Specimens need to be fully labeled with locality, date of collection, collector, foodplant (hostplant or host), and cross-referenced to any photographs, parasitoids, reared adults, or field notes. I assign a unique rearing lot number (including my initials) to each egg or larval collection and associate this number with all my specimens, notes, and photographs. Pencils and indelible inks, such as those found in Pigma Pens, must be used. Heavy-weight archival papers are best; by contrast, notebook paper abrades easily in ethanol.

Unfortunately, caterpillar colors are prone to loss in fluid preservatives—greens fade within minutes of preservation. If a record of the larval coloration is important, then a photograph or an electronic image should be taken.

PHOTOGRAPHY

Even the best vouchers and most detailed notes are no substitute for a living creature—colors and behaviors are best captured with cameras. There are numerous books geared towards insect macrophotography (*see* Shaw 1984, 1987, West and Ridl 1994, Martin 2003, among others). Rather than repeat what you could find elsewhere and in more detail, I will only make a few general comments relative to my experiences with caterpillar photography, having taken most of the images for this guide.

I use a 60mm macro lens with two side flashes that are mounted on a bracketing system. The ability to swing the flashes in close to the lens is especially useful for very high magnification shots of eggs and early instars. For many shots, you may want to scale back the output from one of the flashes to enhance the perceived dimensionality of the subject. A selection of extension tubes (12mm, 20mm, 25mm, and 36mm) are kept at hand, so that I can fill the frame even with tiny caterpillars. The majority of my early images were taken with Kodachrome 25 and 64, but I have since moved to Provia 100 as it does much better with greens. I do not recommend Fujichrome Velvia®—the yellows and oranges are too warm and unreal—an animal in real life should never run second to a film image. Many of my images now are digital.

Caterpillars can be scarce and their lives ephemeral—a gorgeous caterpillar on Sunday could be a drab prepupa or parasitoid victim by Monday morning. Acquire your images as soon as you can and bracket; if appropriate, change the background composition to accentuate the caterpillar's coloration and posture. Slightly underexposed images are easily corrected with imaging software; the details lost in an overexposed image cannot be regained.

Caterpillars are usually very cooperative subjects for learning macrophotography, but some can be annoyingly active. Those that abhor daylight, like cutworms, or that are in their prepupal wandering phase can be maddeningly difficult. Many of these pause briefly if you blow a puff of air over their body. I am not a fan of chilling, but I employ a cooldown period in the refrigerator on occasion. Better substitutes are dark containers and patience. Most caterpillars settle quickly if offered a place to hide or just given a few minutes to find a perch. If I have restless subjects, I put these aside (e.g., in one-pint soup containers or on their own bouquets) and work with others, cycling back and forth until each caterpillar is in a position that would make for a good photograph.

Black backgrounds are dramatic but unnatural and have another drawback: black tentacles, tufts, lashes, and other dark structures blend into the background, or worse, disappear in the image. I prefer natural-light photographs or, when using flashes, to bring backgrounds into close proximity with the caterpillar. Many of the images in this guide were taken with one or two small clamps (left): in the latter case, one to hold the substrate with the caterpillar and a second to position background foliage/matter. For better definition of hairs, especially those that are pale, direct or bounce some light from behind the subject.

Getting a caterpillar completely in focus can be challenging. While setting up for a shot, I often peer over the top of my camera to make sure my lens is in the same plane as the caterpillar (i.e., before looking into the viewfinder). This is also a good opportunity to check the position of your flash(es). Once the image has been composed, rock back and forth several times on your elbows, through the plane of focus, until you know precisely, by feel, when to depress the shutter. Typically you will take the image when the camera's plane of focus is ⅓ of the way through the subject's body. If you do a lot of macro work, you should purchase a macrophotography focusing screen. Cameras that allow you to preview the full depth of field are desirable but not essential. Nearly all of the images in this book were taken with the lens set at f/16, f/22 (with extension tubes the functional *f* may be much higher). A superior alternative to my handheld technique is to employ a tripod with a focusing rail, which allows longer exposure times, precise focusing, and frequently obviates the need for flashes. Caterpillars, being rather sedentary creatures, certainly lend themselves to the tripod option.

Because I try to maximize depth of field and do most of my photography under low light conditions, it is usually necessary to employ flashes. Images taken with natural light are more time consuming, but completely superior. Reflector discs can add much light to your subject—silver reflectors are recommended as they do not bias the colors in your image. (An alternative is to simply cover a piece of cardboard with somewhat crumpled aluminum foil.) Position reflectors at different angles to bring out the texture of your subject. Collapsible varieties fold up and fit into a pouch for easy carrying. Digital cameras, which require less light, should make natural-light photography more routine.

What kinds of images are needed? This and most other caterpillar guides illustrate only one or a few color forms of last instar larvae. For many species, such as the inchworms and tiger moths, a collection of images would be necessary for a taxonomist to sort out which features are of most value in making definitive identifications. Photographic collections of earlier instars are sorely needed, especially for those species where the appearance changes from instar to instar. Egg and pupal images are particularly scarce. While most of the images shown here are dorsolateral views, the serious student is encouraged to acquire dorsal, ventral, and frontal (head) shots for each caterpillar, all of which may prove helpful in identification. Such images can be simple reference shots and need not be natural or aesthetically pleasing images. For example, by confining a caterpillar in a clear CD case, it is possible to get useful images of the insect's venter.

I confess. Most of the images in this guide were taken in my lab using a set of more than 30 props: boxes of sand, trays of leaves, collections of sticks, and an ever-changing bouquet of appropriate background foliage. Natural resting postures and appropriate contexts, especially if associated with careful notes, are far superior. Do not compose false or misleading images—if you find a caterpillar on one plant species, make sure you photograph it on the same. If you encounter your subject wandering on the ground do not put it on a plant to image it, unless you know the plant to be an appropriate foodplant. Lastly, have fun, be creative, and do your best to capture interesting behaviors and other images likely to tell a story or spark an interest in caterpillars.

COLLECTING, VOUCHERING, AND CONSERVATION

Much remains to be learned about the life histories of Eastern moths and butterflies. Even the weekend biologist or student can make worthwhile contributions to our knowledge. As you read through this book, taxonomic problems and uncertainties about the foodplants and life cycles will surface by the dozens: *Acronicta lobeliae*, *Bomolocha*, *Colocasia*, *Cucullia*, *Hyperstrotia*, *Paectes*, *Pyreferra*, and *Spilosoma congrua* are but a handful of those in need of study. Pick a group and start rearing. Take notes, photograph, save voucher specimens as appropriate, and most importantly, share your findings.

The value of saving larval, pupal, and adult vouchers cannot be overemphasized. Well-labeled vouchers are the ultimate reference for a collection or observation. Specimen vouchers can later be examined and reexamined, dissected, or their DNA sequenced. Such is not possible with photographs. An obvious case for the importance of vouchers is seen when a species' taxonomy is still in doubt. The familiar Spring Azure (*Celastrina ladon* complex) is a case in point. What was previously thought to represent a single species is now thought to be a complex of six or more biologically distinct entities. Much published biological or distributional information on the "Spring Azure" now must be reconsidered or, worse, discarded.

Vouchers that are well preserved, labeled, and deposited in a public institution become a scientific legacy. As my colleague Jane O'Donnell often reminds me, "If a picture is worth a thousand words, a specimen is worth a million." Specimen vouchers are of quintessential importance in morphological and taxonomic studies. If one wanted to study microscopic features or examine internal structures, a specimen would be required. Each is its own microcosm of pollen, bacteria, viruses, and other microbes that might be studied in the future. There can be little doubt that long into the future biological specimens will be "mined" for their DNA, each having the importance of a well-preserved fossil. The possibilities are almost beyond our comprehension, e.g., trace amounts of plant material in the gut could be sequenced to determine a caterpillar's diet at the time it was preserved. Toxicological residues in a specimen could be used to study the extent of environmental contamination at some fixed point in the past. Future possibilities will be limited only by the lack of preserved specimens. My vouchers will be my longest legacy. If properly cared for they will be available for centuries—I doubt that any of my books, photographs, or articles will find appreciable use beyond this century's end.

I am an advocate of collecting and rearing and careful observation. These activities are at the same time rewarding and scientifically justifiable, but, just as important, for many children, students, and amateurs, they provide an entry point into the world of entomology, systematics, and invertebrate conservation. Collecting must always be carried out in an ethical and responsible fashion. The collecting policy of The Lepidopterists' Society (http://alpha.furman.edu/~snyder/snyder/lep/) should be read and followed, regardless of whether or not the intent is to release or voucher the reared individuals. While intentions are good, something can always go wrong; never remove more than a fraction (circa 5–10%) of the number of individuals you believe to be present in a population. In those species with very conspicuous caterpillars—for example, some flower-feeding hairstreaks or tent-making nymphalids—it is easy to impact a population through overzealous collecting.

Paradoxically, undercollecting is a greater peril to most Lepidoptera than overcollecting. This is because we still need to know a great deal about most of the species in this guide before we can recognize which might be declining, understand their biological requirements, or develop management practices for their preservation. Outside of the Northeast and Upper Midwest comparatively few moths receive legal protection or are used in conservation planning, simply because we know too little about them. More specimens in collections, more records in databases, and more long-term demographic studies would allow us to identify an appreciably larger set of imperiled species. My State of Connecticut has already lost some 30 species of Lepidoptera. Many of these losses would have been preventable had we known more. Numerous aspects of the life history may be learned by collecting, rearing, and observing caterpillars, e.g., the number of annual broods, cocooning behaviors, and the overwintering stage. We desperately need observations and studies evaluating the impacts of introduced biological control agents on native caterpillars. To my way of thinking, the U.S. Department of Agriculture is far too lenient with what it will allow to be introduced. To permit the mass release in present times of an Asian wasp such as *Pimpla disparis*, whose known host range includes many of our giant silkworms, swallowtails, tiger moths, and members of more than a dozen other families of native Lepidoptera (Schaefer et al. 1989), is unconscionable. Should you become engaged in rearing, an exercise which I find deeply rewarding, remember that an important part of this process is careful observation and good record keeping, so save and label any parasitoids, and share your findings.

CATERPILLAR PROJECTS FOR SCHOOLS, NATURE CENTERS, AND UNIVERSITIES

Caterpillars are ideal for school projects because they are at the same time enormously popular, accessible, attractive, harmless, tolerant of handling, and offer abundant opportunity for real discovery. The metaphors suggested by their developmental changes are powerful and important. Metamorphosis is about change and second opportunities—the ugly duckling story: anything (or anyone) may transform; good things come in little and uncelebrated packages; or conversely, sometimes elegant creatures become average and completely plebian with time. For some, simply watching the pupal transformations will be an epiphany. I am biased, of course, but I regard metamorphosis to be one of the most glorious phenomena in nature. Either the Monarch (*Danaus plexippus*) or Painted Lady (*Vanessa cardui*) make good subjects, because their beautiful adults develop over a period of just a few weeks (and there is no diapause). The former has the advantage of being common and widespread and has considerable associated biology around which to build lesson plans. Its migration biology is marvelous. The Monarch provides a good entry into the phenomenon of mimicry (one of nature's most compelling and obvious examples of organic evolution). Additionally, the massive winter die-offs in its overwintering site will allow the class to discuss conservation issues (e.g., climate change, sustainable use of forests, or the tensions that arise among people with limited resources and immediate needs). Also, children and their parents could be sent out to look for Monarch caterpillars, an activity that by itself is fun and rewarding, even if the caterpillars prove scarce. Painted Lady caterpillars are another option; they are commercially available year-round and can be raised on artificial diet.

Below I suggest some activities and projects that will provide a chance for students to see or work with caterpillars and/or their adults. The initial ones are fine for students of all ages and especially children; the latter five are more suitable for high school and university students.

1) Plant a butterfly garden and include a section for larval foodplants. Milkweeds are a must. Pearly everlasting is a magnet for American Painted Ladies. Bush clover is used by Gray Hairstreaks, Eastern Tailed-blues, and several skippers. Nettles (including stingless varieties) will draw Red Admirals, Eastern Commas, and myriad others. Support native landscaping businesses to the extent possible.

2) Visit a butterfly house or insect zoo. Few facilities allow rearing, but these insectaries provide ample opportunity to talk about metamorphosis, food chains, pollination, and the sustainable use of tropical rain forests.

3) If you have a student who is good with a digital camera that allows close-up imaging, simply collect, rear, and photodocument the life histories of a few species each marking period. Print out (enlarged) color images and post them in the classroom.

4) Raise monarchs and get involved with Orley Taylor's Monarch Watch (http://www.monarchwatch.org/). His Web site has classroom curricula for K-6, instructions for tagging migrating monarchs, life history information, lots of images, and other resources sure to please.

5) Go out with a bed sheet and baseball bat and have the students "beat" tree foliage. Beating invariably provides abundant opportunities to talk about background matching and natural selection, warning coloration, and a laundry list of defensive strategies. Give each participant a clear plastic vial (or yogurt container with clear lid) that can be used to hold the living insect while it is passed around and examined by the students, before it is returned to its foodplant. No need to limit the discussion to caterpillars—trees and shrubs are replete with beetles, stink bugs, spiders, and other interesting animals.

6) Pick a large nearby tree and study its caterpillar fauna intensively: keep a species list of caterpillars that you encounter, record density of caterpillars per leaf or shoot and extrapolate numbers to the entire tree, and estimate seasonal changes in caterpillar biomass. Employ burlap bands around the trunk. If you can borrow a pole pruner with extensions, try comparing canopy versus subcanopy caterpillar densities. Collect feculae samples with funnels to estimate how many caterpillars might be overhead, when they are seasonally most numerous, when they do most of their feeding, etc.

7) Build clay caterpillars of various types (e.g., artificial monarchs and inchworms), tie them out in appropriate habitats, record the frequency and nature of attacks as measured by bill beaks in your clay models. Or build caterpillars with eyespots or snake mimics and see if this affects "predation." Results will vary depending on the size of your models. Experiment.

8) Nest- and shelter-forming caterpillars are environmental engineers that model and shape their environment. Try building artificial leaf shelters and see if your constructions increase caterpillar density and/or diversity and, if so, in what ways.

9) Rear wild caterpillars individually in separate containers and assess the local parasitoid fauna. What percentage of caterpillars is parasitized? Work with a taxonomist to get your parasitoids identified. Are a substantial number of your parasitoids introduced biological control agents? What are the parasitism rates of brightly or warningly colored species relative to cryptic ones?

10) If your town is using pesticides, e.g., spraying for mosquitoes, try rearing families of caterpillars (e.g., from a single clutch of eggs) on sprayed leaves versus those you believe to be free of pesticide and compare survival. Alternatively, get some foliage from a genetically engineered crop and assess its impact on a range of pest and non-pest species.

USING THIS GUIDE

Family order follows Kristensen (1998). Within families, I follow Hodges *et al*. (1983) or use an alphabetical listing. Species within a genus are usually presented alphabetically, with some exceptions to keep similar appearing species together. Families (and some subfamilies) are introduced with information about their diversity, diagnostic features, and life history, and then conclude with collecting and rearing tips. Short summaries are sometimes used to introduce more important tribes and large genera. Because of space limitations, much information that is rightfully introductory in nature is sprinkled into the species accounts—the reader is urged to cast about the Remarks section of the species accounts to locate information with relevance across a given family.

Italics are used in the Recognition section to emphasize reliable and readily observable characters. Keep in mind that coloration and patterning can be highly variable (e.g., in the inchworms and tiger moths). It is always advisable to back up and read the family account to make sure your caterpillar agrees with characters given there. The diagnosis is intended only for last instars (e.g., it is next to useless for many penultimate dagger moths). Use coloration with caution, especially if the feature is not in italics. In many cases, I have "over-diagnosed" a species, simply because I have not yet seen the extent of variation common to a species. Body lengths are approximate—sometimes they have been estimated from the adult forewing measurements given in Covell (1984) and the relative body proportions of a given species of caterpillar. Following the length measurement, earlier instars or similar and related species are introduced.

The Occurrence section provides information on habitat, distribution, and number of annual generations. This information is poorly known for many of the moths in this guide and should be used cautiously—e.g., as one moves southward, the number of annual generations gets especially confusing and inexact. As a matter of convention, I generally circumscribe the range beginning with the northwestern portion then move in a clockwise direction. The emphasis is entirely on the eastern portion of a species' range; only occasionally do I make mention of its presence farther west or south.

The plant on which a caterpillar is found often provides a singularly valuable clue to its identity. But be cautious in assuming that the plant on which a caterpillar is discovered is, *de facto*, the foodplant. Prepupal, diseased, and parasitized caterpillars wander; caterpillars drop from their perch if alarmed; many shrub- and tree-feeding species descend into proximate vegetation during the day. In the list of Common Foodlants, I have not attempted to list all known foodplants, especially for species I regard to be polyphagous. My reviewers and I made a special effort to ferret out erroneous foodplant records and offer new or corrected information. An especially important resource with regard to foodplant records is Robinson *et al*.'s worldwide compendium of lepidopteran foodplants (http://www.nhm.ac.uk/entomology/hostplants/).

Be advised that foodplant use varies considerably across a species' range. A strict lupine specialist in New England may only eat vetch elsewhere. Magnolia is favored by the Eastern Tiger Swallowtail (*Papilio glaucus*) in North Carolina, while cherry receives more eggs in Connecticut. Blues and hairstreaks are well known for their tendency to be locally specialized but regionally generalized in diet. Another point to keep in mind, which is especially relevant to rearing caterpillars, is that many captive-bred species may consume and grow rapidly on foodplants that are seldom, if ever, used in nature. In your notes, e-mail posts, and especially published reports, differentiate between natural foodplants and those on which a captive larva was lab-reared.

The Remarks section is a hodgepodge of taxonomy, biology, economic entomology, and anything else that seemed interesting or relevant. The only consistent component is that I comment on the overwintering stage near the end of each species account, unless this information is uniform for an entire family, tribe, genus, etc., and has been mentioned previously.

Remember that information relevant to a species may often be found in the accounts of related species. For a few butterflies and moths the overwintering stage was a best guess, based on the specimen data and conversations with other workers.

Larval and adult voucher specimens for this work have been deposited at the University of Connecticut. The specimens used for the adult images in this guide bear a label denoting such. Data for adults (State only) and larvae (locality, date of collection, foodplant, collector, and photographer) are posted on my Web site at the University of Connecticut and digital copies are available upon request.

If you cannot find your caterpillar in this guide you might also search Old World literature. The lepidopteran fauna of Europe and Asia is more thoroughly studied and there are several books that illustrate hundreds of caterpillars in color: e.g., Sugi (1987), Porter (1997), and Beck (1999). While the caterpillars figured in these volumes will be specifically distinct from those in our fauna, in many cases, they can narrow your search to a genus or set of related species.

CLASSIFICATION AND NOMENCLATURE

The scientific name of all organisms includes two parts: the generic and specific name. The genus is always capitalized and the species name is given in lower case letters; in printed materials the scientific name is placed in italics, underscored, or in some other way distinguished from surrounding text. When a scientific name is repeated in the body of a single page or paragraph, the genus name may be abbreviated by using the first letter only, e.g., *Alsophila pometaria* may appear as *A. pometaria*. Rarely only the specific name is used. Every organism has a unique scientific name but may have multiple common (vernacular) names. For example, adult and larval stages often have different monikers. The Corn Earworm is also known as the Cotton Bollworm, Soybean Podworm, and Tomato Fruitworm. The species in this guide that are found in Quebec have a French common name. I generally tried to provide a common (English) name and a recently accepted scientific name, except where to do so proved awkward. Common names were drawn largely from Covell (1984); a few were created for this guide.

In the Linnaean system, all animals are classified in seven categories: kingdom, phylum, class, order, family, genus, and species. Butterflies and moths comprise the order Lepidoptera within the class Insecta. Representatives of 24 families are illustrated in this guide. Additional categories, beyond the seven obligatory ranks (e.g., superfamilies and subfamilies, and tribes), are frequently interpolated in classifications, especially in large or heterogeneous taxonomic groups.

CATEGORY	LATIN NAME SUFFIX	EXAMPLE	COMMON NAME SUFFIX	EXAMPLE
Superfamily	-oidea	Noctuoidea	-oids	noctuoids
Family	-idae	Noctuidae	-ids	noctuids
Subfamily	-inae	Hadeninae	-ines	hadenines
Tribe	-ini	Xylenini	-ines	xylenines
Genus	variable	*Lithophane*	not applicable	pinions

HELPFUL WEBSITES

BioQuip: (This biological supply house specializes in entomology gear and supplies.)
http://www.bioquip.com/

The Caterpillars of Guanacaste:
http://janzen.sas.upenn.edu/caterpillars/database.lasso/

HOSTS—a database of the hostplants of the World's Lepidoptera:
http://www.nhm.ac.uk/entomology/hostplants/

The Lepidopterists' Society:
http://alpha.furman.edu/~snyder/snyder/lep/

Monarch Watch:
http://www.monarchwatch.org/

North American Butterfly Association:
http://www.naba.org/

The Xerces Society:
http://www.xerces.org/