Owlet moths represent one of the most successful branches on the tree of life, whether measured in terms of species numbers, mass, or ecological importance. Adults range in size from a little over 7 mm to what may be the New World's largest insect, the White Witch (*Thysania agrippina*), which has a wingspan that sometimes exceeds 30 cm. Noctuoid taxonomy and classification is undergoing a renaissance. Current classifications differ markedly in the number of recognized families and subfamilies for this group of moths. The Noctuidae have been treated as a single family historically, but now are frequently divided into smaller and more natural assemblages, with the resulting classifications differing among workers. Moreover, both molecular and morphological studies indicate that the tiger moths (Arctiidae) and tussock moths (Lymantriidae) are evolutionary derivatives from *within* the Erebidae. Here, we follow Lafontaine and Schmidt's (2010) recent reclassification and checklist for the North American fauna in which four families are recognized: Erebidae, Euteliidae, Nolidae, and Noctuidae. We refer to this group collectively as owlets or Noctuidae *sensu lato* (Noctuidae *s. l.*). We did not include the Arctiinae and Lymantriinae, now two erebid subfamilies, because the common eastern representatives of both groups were treated in Wagner (2005). This book illustrates 726 species of eastern noctuoids, of which 372 species are accorded full (page) accounts; an additional 89 species are diagnosed or in some other way made identifiable. Our western boundary is the hundredth meridian as it was for Klots (1951), a work that greatly influenced the early interests of the first three authors. Each treatment includes a diagnosis, brief notes regarding similar species, common habitats, an approximate range, phenology, a statement about relative abundance, a brief accounting of larval foodplants, and a Remarks section that is a potpourri of life history, taxonomy, and other relevant notes. For most of these species, we include two adult images, one of a live individual in a representative resting posture and one of a spread specimen. An additional 354 species are treated in abbreviated accounts (without adult images). The set of species selected for inclusion emphasizes taxa likely to be encountered by the layperson or forest manager, attractive species apt to draw public attention, and those of economic significance. A number of scarce or otherwise obscure species are included simply to provide better taxonomic coverage, or because they have interesting life histories, are of conservation concern, or have caterpillars that we otherwise deem noteworthy. Tree- and shrub-feeding taxa, such as the daggers, quakers, pinions, sallows, zales, and especially the underwings (a popular group with collectors), are richly represented.

Introductory sections address the importance of owlets, morphology, larval diets, natural enemies, classification, and various topics related to finding and rearing owlet caterpillars. Within the body of the work, each of the subfamilies, most tribes, and several large genera are introduced separately. The book concludes with two indexes: one for foodplants and a combined taxonomic/subject index.

Our target audience is intended to range from students or laypeople to Ph.D. entomologists with training in systematics. An overarching goal was to prepare a guide that could serve as a portal into the world of lepidopterology (the study of butterflies and moths) for those without training in biology. To make this possible we offer extensive introductory text,

BIRDS AND CATERPILLARS (AND CLIMATE CHANGE)

The arrival of birds to temperate forests each spring is timed to coincide with peak insect biomass. The numbers and weight of nestlings that can be reared, the rapidity of their growth, and the number of broods attempted are all influenced by the amount of food available to the nesting parents. In temperate forests, much of the insect forage is made up of caterpillars (Nagy and Holmes 2005, Rodenhouse and Holmes 1992), especially those of inchworms (Geometridae), leafrollers (Tortricidae), and owlets. Most of the owlet caterpillars available to foliage-gleaning birds come from just three of the 63 or so tribes represented in this work: the Orthosiini, Hadenini, and Xylenini (all Noctuinae). Daniel Janzen, who has studied caterpillars for more than two decades in the tropics, refers to caterpillars as the hamburger of forested ecosystems. While graphic and rich, the metaphor understates the importance of caterpillars to birds—we venture that caterpillars make up no less than 60% of the diet of many songbird nestlings. One of the dangers of climate change is that some plants and animals will find themselves mismatched with the seasonal or phenological cycles upon which their survival is dependent. When spring comes early, most insects can adjust, because much of their vernal activity is triggered by ambient temperatures. But, migratory birds wintering in the Caribbean or Latin America are timing their migrations, courtship, mating, and nesting activities by changing day lengths, oblivious to whether or not eastern North America is experiencing an earlier-than-average spring. Phenological mismatching and diminished nestling success tied to climate change has been documented in the great tit (Visser et al. 2006) and several other species in Europe. The extent to which this phenomenon is challenging birds and other wildlife elsewhere is in much need of study.

■ Eastern bluebird on way to feed nestlings. ■

emphasize common names, provide images of the live insects, infuse the species accounts with natural history and information of general interest, and offer an extensive glossary. We hope that we have not fallen short, as so much remains to be learned about these moths.

Importance of Owlet Caterpillars and Adults

By virtue of their sheer diversity and abundance, owlet caterpillars and adults have become enmeshed in the ecological processes of forests, grasslands, and other terrestrial ecosystems. Owlet caterpillars are common on trees and most woody plants in the spring, when foliage is soft and rich with nutrients. Another peak of larval abundance occurs in late summer and fall, mostly on composites and grasses.

Caterpillars are a staple for insectivorous vertebrates. Birds are particularly reliant on caterpillars, and many insectivorous species time their nesting activities to periods of peak larval abundance—nestling survival would be appreciably lower in forests lacking owlet larvae (see essay on page 9). Goatsuckers move with storm fronts to feed on the abundance of moths that push northward on the leading edge of tropical storm cells—we estimate that greater than 90% of the moth biomass in these migratory swarms is made up of armyworms (*Mythimna* and *Spodoptera*), loopers (various Plusiinae), flower moths (*Helicoverpa* and *Heliothis*), the Black Snout (*Hypena scabra*), cutworms (*Agrotis ipsilon* and *Peridroma saucia*), and other owlets.

Insectivorous mammals, including mice, shrews, raccoons, skunks, foxes, and many others, consume cutworms and other owlet caterpillars (and their pupae) found near the ground; some mice ascend shrubs and trees during their nocturnal forays for insect prey. Some insectivorous bats are dependent on moths and, by default, noctuoids. The colony of Mexican free-tailed bats that roosts under the Congress Avenue Bridge in Austin, Texas, is said to harvest more than 35,000 pounds of insects during the course of some nights. And the colony of 20 million Mexican free-tails that pours forth at twilight from Bracken Cave, Texas, purportedly consumes more than 100 tons of insects each night before returning to its roost. No doubt a healthy fraction, and perhaps the largest, is made up of noctuoids. Even mammals as large as bears feed on cutworm adults. Of particular importance are aggregations of the Army Cutworm (*Euxoa auxiliaris*), which aestivates by the millions in talus slopes in the Rockies. The communal gatherings are a critical food store for the grizzly bears of Yellowstone National Park and presumably for bear populations elsewhere. A single bear is estimated to eat 20,000 to 30,000 moths a day during portions of the summer—as much as one-third of the calories required for an entire year may derive from the consumption of owlet moths (Mattson et al. 1991; French et al. 1994; White et al. 1998a, b).

The pollination services provided by noctuoids are underappreciated (Committee on the Status of Pollinators in North America 2007). Many cuculliines, hadenines, heliothines, plusiines, xylenines, and myriad others avidly seek nectar at flowers. Owlets are among the most common insects to visit flowers of apple, apricot, aster, basswood, buttonbush, campion, cherry, fireweed, goldenrod, jasmine, lobelia, milkweed, various orchids, phlox, pinks, red maple, wild plum, willow, white snakeroot and other eupatoriums, as well as other plants that offer nectar at night. Noctuidae may be the principal pollinators of *Platanthera* and other white-flowered orchids. *Cucullia* are able to take nectar while hovering, much like hawk moths (Sphingidae); similarly, plusiines scarcely alight, placing just their tarsi on the corolla while feeding. Other owlets, like xylenines, orthosiines, and hadenines, actively crawl over flowers while probing them with their relatively short tongues.

Larvae of some owlets are macrodecomposers that consume and digest fallen leaves, wood, and other organic matter. Herminiines are especially important in this regard with more

■ Grizzly bear flipping rocks to uncover aggregations of the Army Cutworm *Euxoa auxiliaris*. ■

than 50 common, litter-feeding species in the East—the subfamily can be abundant in deciduous woodlands. One owlet serves as a biological control agent in our region: the Toadflax Brocade (*Calophasia lunula*) was introduced into Belleville, Ontario, to control butter-and-eggs, an introduced *Linaria* species. The moth has since spread south to at least Maryland. No less than two are used in biological control programs elsewhere.

Because of their great diversity and relative ease of sampling and identification, noctuoids are used in biotic assessment and monitoring efforts. Across the East, and especially in the Northeast, noctuoids and other moths are taken into account by The Nature Conservancy, Natural Heritage Programs, state agencies, and like-minded organizations when considering land acquisition, management plans, and other conservation decisions. In Connecticut, 42 (54%) of the 78 lepidopterans listed as endangered, threatened, or of special concern are owlets (including tiger moths).

The indirect effects of plant-animal interactions on the quality and culture of our day-to-day lives are too commonly overlooked. Some of our most pleasant fragrances, such as jasmine—a staple of the cosmetics industry—are volatiles produced and released to attract moths and other nocturnal pollinators. The sweet scents of gardenia, narcissus, and other flowers that we select for our bouquets and corsages are manufactured by plants to attract moths. The spices that flavor our food are secondary chemicals produced by plants to discourage herbivory by caterpillars and other enemies. Similarly, the turpentine, resins, and latexes manufactured by plants repel the legions of insects and pathogens that would otherwise despoil unprotected tissues and organs. Antiherbivory substances may have considerable pharmaceutical value: e.g., digitalis, salicylic acid (aspirin), and taxol. Hundreds of plant alkaloids such as nicotine, caffeine, and theophylline shape the culture of our daily lives. Among the most widespread defensive compounds in woody plants are tannins; these phenolics are cross-linked to proteins, rendering ingested plant tissues indigestible. Humans have found other uses for tannins, as in the production of leather and red wines. In sum, such indirect effects of Lepidoptera have been great, and our collective human experiences much enriched.

While the vast majority of owlets should be regarded as having a positive or inconsequential economic importance, the ranks of the Noctuoidea include more than two dozen significant agricultural and garden pests in the East. Armyworms (*Mythimna* and *Spodoptera*) occasionally reach densities so great that they lay bare acres of cereal and other field crops. Members of the genus *Spodoptera* become increasingly important southward and at times cause massive crop losses. Cutworms, so named because of their habit of severing young plants at or near ground level, can be particularly detrimental in the spring when a single larva may consume or otherwise damage many seedlings over the course of its development. Both garden and field crops are adversely affected, e.g., some loopers (Plusiinae) are serious pests of crucifers. Heliothine noctuids are flower and seed predators. The Corn Earworm (*Helicoverpa zea*) and Tobacco Budworm (*Heliothis virescens*) account for millions of dollars in annual crop losses across the United States. These two moths and most of the other owlets regarded as crop pests are migrants that move northward en masse from our southernmost states, Mexico, and the Caribbean on the winds of storm fronts that boil out of Mexico and the Gulf. Single storms carry millions of individuals—local and regional population eruptions sometimes follow, resulting in minor to complete defoliation of susceptible foodplants.

Curiously, no native eastern noctuoid is a chronic forest pest and only rarely do any cause defoliation in forested ecosystems. In Canada, the Straw-eyed Tentmaker (*Enargia decolor*) occasionally strips aspen of all leaves (Wong and Melvin 1976). The Black-dotted Brown (*Cissusa spadix*) and Common Oak Moth (*Phoberia atomaris*) sometimes defoliate oaks over localized regions, and in the South and West, a number of melipotis sometimes strip their leguminous hosts of leaves. In all cases outbreaks are localized and ephemeral. The Gypsy Moth (*Lymantria dispar*) is the principal owlet known to defoliate tracts of forests across eastern North America, but it is an exotic lymantriine introduced from Europe and falls outside the coverage of this work.

Caterpillars of a few acronictines, and especially those of the American Dagger (*Acronicta americana*), may tunnel into siding and other wooden structures to fashion pupal cells, thereby blemishing outdoor structures and furniture. Florida's Cabbage Palm Caterpillar (*Litoprosopus futilis*) is a more significant nuisance. Wandering prepupal larvae release a reddish-brown fluid that deeply stains siding and other nearby objects; some enter structures, including homes, in search of suitable pupation sites. Cocooning *Litoprosopus* caterpillars

A NOTE ON NOMENCLATURE

Suffixes for family-group and tribal names are standardized across all zoological classifications (see below). Common or vernacular names based on the scientific higher category names may be made by adding English suffixes (right-hand column in table). The first letter of higher category names must be capitalized (e.g., Acronictinae). Capitalization is optional for the common name based on this name (Acronictines or acronictines).

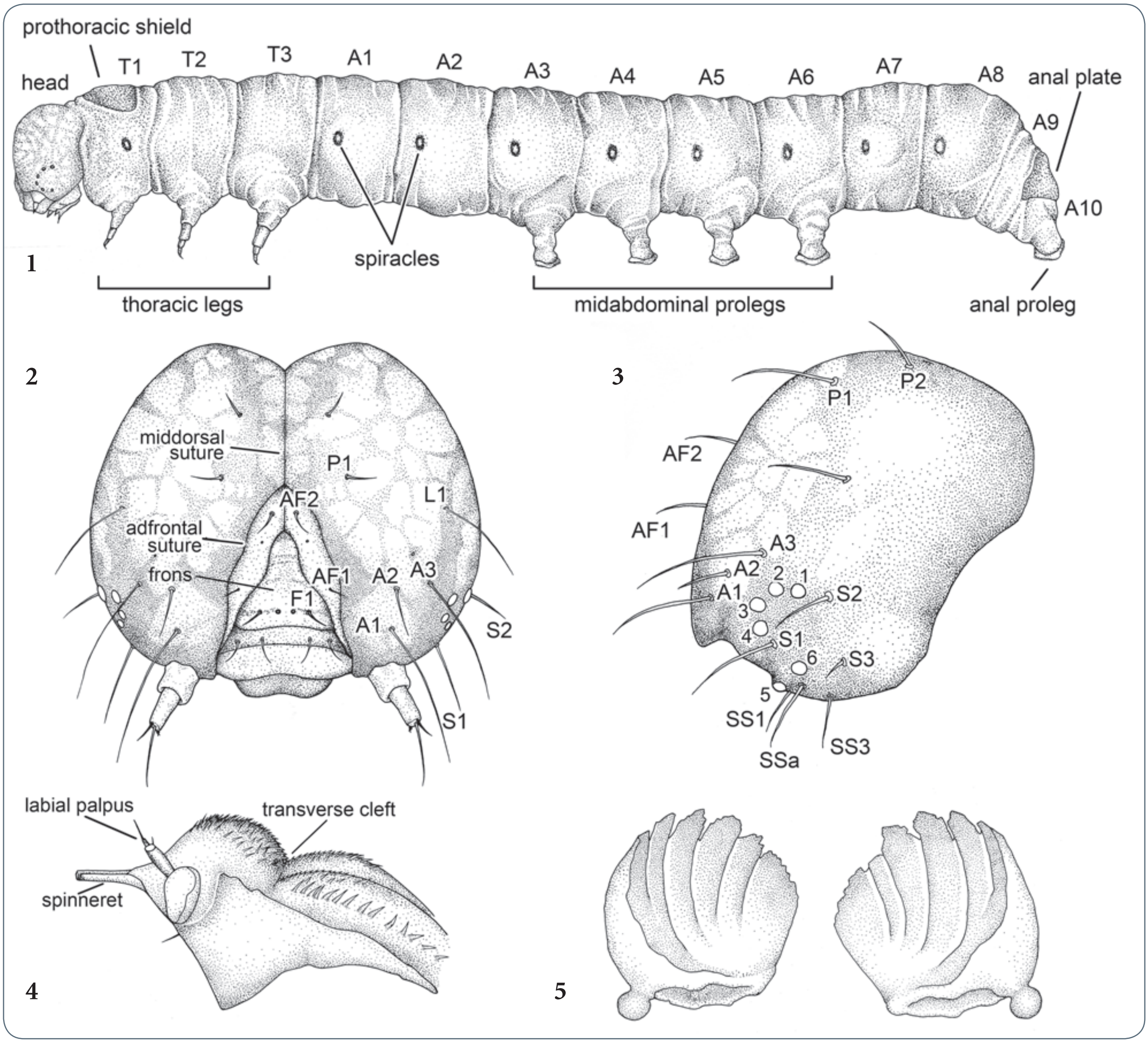
Category	Latin suffix (example)	Latinized suffix common name (example) (English common name)
Superfamily	-oidea (Noctuoidea)	-oids (noctuoids)
Family	-idae (Noctuidae)	-ids (noctuids) (owlets) (in part)
Subfamily	-inae (Noctuinae)	-ines (noctuines) (cutworms, sallows, and kin)
Tribe	-ini (Xylenini)	-ines (xylenines) (pinions, swallows, and kin)
Subtribe	-ina (Antitypina)	-ines (antitypines) (no common name applied)

tear up rugs, upholstery, and other fabrics, and then weave the severed fragments into the walls of their cocoons.

Adult owlets are rarely considered pests in the East, although in the Rockies, millers (mostly the Army Cutworm, *Euxoa auxiliaris*) sometimes aggregate by the thousands in garages, sheds, and other structures. In our region, aestivating individuals of the Copper Underwing (*Amphipyra pyramidoides*) will gather in large numbers under shutters and in other man-made structures. Their liquid excreta can be substantial, accumulating on shutter slats, siding, and adjacent outdoor furniture; fortunately the reddish staining is easily washed away.

Morphology

Like all insects, caterpillars have three body sections: head, thorax (segments T1, T2, and T3), and abdomen (segments A1–A10) (Fig. 1). Because the thorax and abdomen are little differentiated in caterpillars, they are sometimes collectively referred to as the trunk or body. The head (Figs. 2–3, 6–8) is comparatively simple and unmodified; it is usually rounded, and either smooth and shiny or granulated in texture. An important landmark is the **triangle** or **frons** (Fig. 2), which is bounded

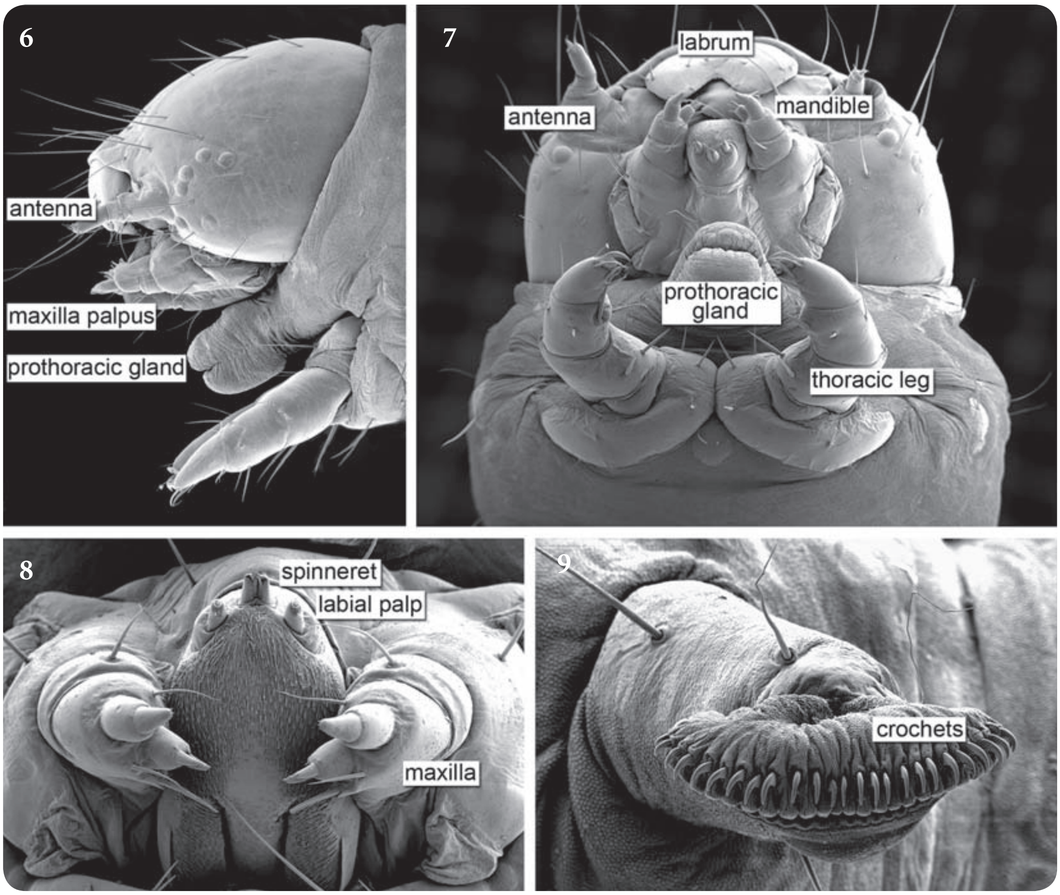


■ **Larval morphology.**
Fig. 1: Lateral view of whole body. **Fig. 2:** Frontal view of head. **Fig. 3:** Lateral view of head.
Fig. 4: Hypopharyngeal complex. **Fig. 5:** Mesal or inner surfaces of mandibles. ■

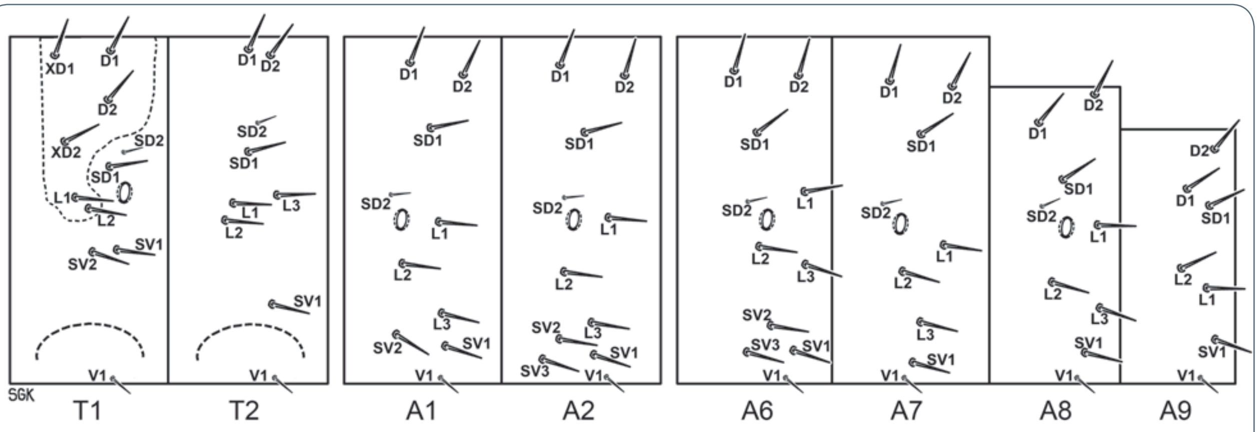
on its sides by the **adfrontal sutures**. The height of the triangle relative to the length of the **middorsal suture** is constant within a species and is sometimes used to diagnose members of a genus. Many owlet caterpillars have an elongate, darkly pigmented patch, the **coronal bar**, to either side of the middorsal line. Caterpillars have six **stemmata** or **lateral eyes** on each side of the head, more or less arranged in a semicircle, with the fifth displaced toward the base of the antenna (Figs. 3, 6)—the relative size and spacing of the stemmata differs among owlet tribes and subfamilies. The relative length of the **antenna** also varies among groups. The mouthparts, unsurpassed in their importance to larval taxonomists, are not given their due in this work, because they often must be dissected and examined under a compound microscope.[1] The **mandibles**, and in particular their inner surfaces, provide many useful species-level characters; details of the **hypopharyngeal complex** (Figs. 4, 8), e.g., number and development of spines over the upper surface, are routinely used by specialists to verify species-level identifications. Features of the **spinneret** and **labial palpi** (Fig. 8) also may be of value in making determinations. The various forms of the spinneret (e.g., the position of the pore, whether or not it bears flanges, to what degree its apex is fringed, or the presence of a dorsal groove) have much taxonomic value at the subfamily level. The spinneret's length, relative to that of the labial palpus, is also diagnostic for many species, genera, and tribes.

The thorax is composed of the three leg-bearing segments. The degree to which the **prothoracic shield** is differentiated from adjacent areas of T1 (prothorax) varies across and within subfamilies. In owlets that feed on foliage, the shield may be scarcely differentiated. The opposite extreme occurs in many borers where the shield is sclerotized (blackened) and conspicuous in relation to the rest of the thorax. The dorsum of the last abdominal segment bears a variously modified **anal plate** or shield. (Both the prothoracic and anal plates provide a rich source of taxonomic characters for some groups, especially among those that are internal borers.) **Spiracles**, the ventilation openings into an insect's respiratory system, are found on segments T1 and A1–A8, with the first and last spiracles enlarged. The spiracular color, though variable, is often used in identification. Many workers use the height (longest diameter) of the spiracles as a standard against which the lengths of the body **setae** (hairs) are measured. As in other caterpillars,

[1] Godfrey (1987: 4) provides a simple protocol for preparing dissections of the mandibles and hypopharyngeal complex. Sometimes it will be helpful to clear and stain preparations, using potassium hydroxide and stains in the same way that they are used for studying genitalia.



■ Scanning electron micrographs of the Androgea Armyworm (*Spodoptera androgea*). **Fig. 6:** Lateral view of head. **Fig. 7:** Ventral view of head and T1. **Fig. 8:** Dorsal view of mouthparts; note dorsal groove in spinneret (characteristic of cutworms and other higher Noctuidae). **Fig. 9:** Proleg with *circa* 26 crochets. ■



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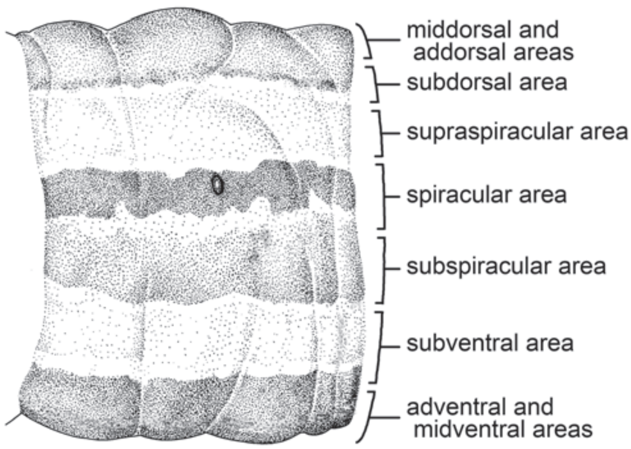

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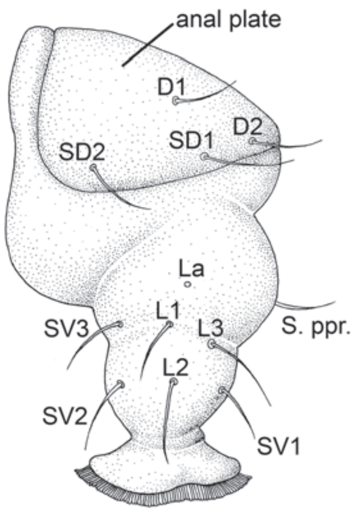

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■ **Larval chaetotaxy and patterning.**
Fig. 10: Schematic diagram of first two thoracic and six abdominal segments showing names for primary setae.
Fig. 11: Trunk regions. **Fig. 12:** Lateral view of A10 with primary setae indicated. ■

prolegs are usually present on A3–A6 (collectively called the midabdominal prolegs) and on A10 (anal prolegs), although the anterior pairs are frequently reduced in owlets (e.g., many erebines, Condicinae, and others) or are absent entirely (e.g., Acontiinae, Bagisarinae, many Hypenodinae, most Plusiinae, etc.). (Early instars of many trifids have reduced prolegs on A3 and A4.) The apex of the proleg bears a series of hooks called **crochets** (Fig. 9). The individual crochets being either one length (uniordinal), or two alternating lengths (biordinal), help assign a caterpillar to a tribe or subfamily. While the number of crochets on a given proleg may differ between closely related species, we seldom refer in this work to characters of the crochets, again because larval preservation and microscopic examination are needed to assess crochet number and character, and because numbers often vary within a species.

We use the term **stripe** for 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**, **subventral**, **adventral**, and **midventral** stripes (Fig. 11).[2] Markings that extend around the caterpillar's body are called **rings** or, when thicker, **bands**. **Line** is used for shorter markings, regardless of their orientation.

Chaetotaxy refers to the presence or absence, relative lengths, and positions of the body setae. Formal keys for the identification of caterpillars are heavily dependent on

[2] We use these terms to define relative position on a hypothetical cylinder and, for the purposes of this text, ignore arguments of homology based on setal insertions or studies of larval development.

chaetotaxy, particularly the **primary setae**, i.e., those that are broadly homologous across lepidopteran families. A few lineages also possess additional **secondary setae**. The primary setae have specific names based on their position (Figs. 10, 12) (Hinton 1946, Stehr 1987). The basic number of primary setae on a body segment is eleven: two dorsal (D1 and D2), two subdorsal (SD1 and SD2), three lateral (L1–L3), three subventral (SV1–SV3), and one ventral (V1) (Fig. 10); this number varies between segments (e.g., the prothorax bears two additional setae, the XD1 and XD2, and many of the 11 primary setae are lost rearward of A8). Variation in number and position occurs among species, genera, and families; accordingly, setal arrangements are often used in taxonomic diagnoses. For example, the SD1 seta on A9 is undifferentiated from other dorsal or lateral setae in most erebids (it may be greatly thinned in some euclidiines) and basal noctuids, but it tends to be appreciably finer in some plusiines, hadenines, noctuines, and their kin. Serious students will find chaetotaxy invaluable, and will want to consult Stehr (1987). Thoracic and abdominal setae are borne from **pinacula**, the rounded, hardened bases that are often more darkly pigmented than adjacent cuticle. A glossary with biological, morphological, and other specialized terms is provided at the end of this book.

Larval Diets

Where there are terrestrial plants there are owlet caterpillars: nearly all woody plants, grasses, most forbs, and even ferns host one or more species. In addition, algae, fungi, lichens, leaf litter, and various other organic substrates are exploited. Although none of our eastern owlets is truly aquatic, a number feed on aquatic plants, and our divers (*Bellura*) are reported to be capable swimmers. Numerous lineages, especially among the Noctuidae, are denizens of early successional habitats: grasslands, meadows, weed lots, and coastal strand communities. Included in this same set of species are several agricultural pests and the unwelcome owlet caterpillars that frequent our vegetable gardens.

Fewer noctuoids than might be expected feed on shrubs, trees, and other woody plants, although these include several diverse groups with many species: e.g., daggers (*Acronicta* and kin), underwings (*Catocala*), zales, pinions (*Lithophane*), and other xylenines. Many owlets that feed on woody plants are univoltine species that are dependent on young leaf tissues in the spring. Members of two tribes, the pinions and sallows (Xylenini), and the arches, quakers, and kin (Orthosiini), are among the most abundant spring-feeding forest macrolepidopterans and no doubt play an important role in the spring diets of insectivorous birds and mammals. Exceptions are many: daggers (Acronictinae), yellowhorns and kin (Pantheinae), and some others feed on mature, hardened foliage of shrubs and trees—as might be expected, their caterpillars tend to have large heads and mandibles.

Leaf litter of varying degrees of dampness and decomposition is consumed by various erebids and noctuids. Some noctuines that overwinter as caterpillars consume fallen leaves during the winter and spring. Many Herminiinae feed on downed plant matter and senescent, aboveground organic matter. Included among the litter moths are two of our most specialized owlets: *Idia majoralis* is apparently an inquiline in pack rat (*Neotoma*) nests, and *Idia gopheri* is a denizen of gopher tortoise and armadillo burrows where its caterpillars feed on droppings. Algae and lichen feeders include lichen punkies (Afridinae), some halflings (Hypenodinae), litter moths (Herminiinae), midgets and kin (Elaphriini), *Metalectra*, and others (see Wagner et al. 2008b). Several genera feed on fungi, e.g., *Chytonix*, *Metalectra*, and presumably a number of halflings.

Of the 815 eastern owlets treated here, only a few genera have carnivorous members; these include *Cosmia*, *Elaphria*, *Enargia*, and *Lithophane*, all of which are facultative predators (they can and often do mature on leaf tissue). Predaceous owlet caterpillars feed principally on other lepidopteran larvae and pupae, especially those that are appreciably smaller or otherwise vulnerable (e.g., in or near a molt). Scale insects and other sessile Hemiptera are also consumed. In addition to the above are those species that are facultatively cannibalistic. Such behavior is frequent in flower and seed feeders, stem and root borers, and among taxa where the food supply may be limited and/or the risk of movement to a new feeding site is high.

Finding Caterpillars

The most sporting and rewarding means of finding caterpillars is to discover them individually by examining leaves, flowers, stems, and bark; by opening shelters and galleries; and by conducting other direct visual searches. In so doing, one learns about the animal's feeding and resting behaviors, its alarm responses, and other basic aspects of a caterpillar's biology. (Some of our colleagues whimsically refer to such searching efforts as "zenning" for caterpillars.) Watch for signs of feeding, especially damaged leaves and feculae (droppings). New growth or actively growing plants are often favored. Additional tips on locating caterpillars are given in Wagner (2005) and references therein.

Sizeable evolutionary radiations of grass feeders are found within the Erebinae, Eustrotiinae, and Noctuinae (Apameini, Hadenini, Leucaniini); dozens of genera scattered across other owlet subfamilies can be added to these. Grasses are important winter foods for some Noctuinae that later switch to feeding on forbs or even woody plants as they become available in the spring. Most grass feeders feed on the blades, but some specialize on the flowers and seeds. Numerous apameines bore into stems or roots or feed externally on these tissues, belowground. Grass feeders are cryptic in both coloration and habit and may shelter in concealed sites by day. Nighttime searches will be more productive. Taller grasses can be sampled with a beating sheet or sweep net. Species that stay within a hummock or feed close to the ground will have to be rooted out individually.

A large guild of species (especially among the apameines) either bore into aboveground tissues or tunnel belowground in rhizomes and roots. The most familiar of these is the large genus *Papaipema*, with more than 50 eastern species. Their presence is usually revealed by the frass that is pushed from the larval tunnel and accumulates on the ground below the tunnel entrance. Related genera with species that tunnel in roots are far less conspicuous in habit and poorly known. A great many apameines are specialist feeders on grasses, sedges, and related plants—wetlands have a rich fauna. Locating larvae requires special effort, but the potential to make new and worthwhile biological discoveries is great.

As a group, owlet caterpillars tend to be cryptic in both coloration and habit, and many are nocturnal. They can be exceedingly difficult to locate by day, hiding in shelters, in bark fissures, and beneath leaf litter or, in the case of many cutworms, tunneling belowground. Expect nocturnal searches to yield different sets of species than those recovered from leaves during the day. Beating or sweeping is usually the most efficient method for sampling noctuoid caterpillars, as explained below. Given that all Lepidoptera are more abundant as earlier instars and early instars are more apt to rest on foliage, it pays to keep a watchful eye for young caterpillars. Learn to distinguish small and early instar noctuoids from their more numerous microlepidopteran cousins. Many microleps possess a clearly demarcated prothoracic shield, and most have the ability to wriggle or scoot backwards, often with great rapidity (see Wagner 2005: 11 for additional tips for distinguishing between macrolepidopterans and microlepidopterans).

Members of several lineages perch on bark during the day, and coloration is often a clue to their identity. In general, green caterpillars will be found resting on foliage and other green tissues. Bark-resting caterpillars tend to be gray or brown, and are often hairy or have rootlet setae along the subventer; many are either somewhat flattened or have the ability to flatten their bodies. Beating is an effective technique for acquiring bark resters (especially those that position themselves along twigs and branches). Burlap banding also works well. At eye level, wrap a six-inch-wide band of burlap around a stem/trunk twice. Cut slits up from the bottom to within an inch of the upper edge of the burlap "skirt" or bands so that flaps of the material can be lifted and the bark beneath examined (right). The method works best on smooth-barked trees, and is all but useless on shagbark hickory and other trees that have an abundance of refugia. Of course, different tree species host different caterpillars. Don't expect to find more than a caterpillar or two for every ten skirts on a given day. Late spring, before foliage has hardened, is the most productive season. Dale Habeck had moderate success sweeping tree trunks with a soft-bristled hand broom or wide paintbrush over a beating sheet.

More so than for other Lepidoptera, searching on the ground, belowground, or on objects near the soil surface can be a fruitful means of locating erebid and noctuid caterpillars. By day, cutworms secret themselves on the ground (some even beneath it), and then emerge from their hiding places after nightfall to feed. A number seek shelter under objects, especially the grass and forb feeders. To find these, flip boards, logs, rocks, fallen vegetation, trash, and leaves in contact with the ground. We have not deployed small squares of wood or other sheltering objects, but these have been used by others to acquire cutworms and other caterpillars. In agricultural fields, Crumb (1929) collected larvae under bundles of cut vegetation that he had strapped together and placed out as "bait." When looking for caterpillars in low vegetation, we avoid areas where mouse runways are plentiful.

Members of *Agrotis*, *Euxoa*, *Striacosta*, and a few *Schinia* hide belowground during the day. The Sandhill Cutworm (*Euxoa detersa*) illustrated in this work was found while screening sand. Friable and/or sandy soils are more likely to produce caterpillars than clays and other dense soils. Larval coloration and form are a clue to habit—stocky, pale to brown caterpillars with a smooth integument, inconspicuous setae, and short prolegs are often diggers that tunnel underground.

As noted above, leaf litter can be searched. During the growing season, check around the bases of trees, especially below those with smooth bark that lack an abundance of hiding sites along the bole. Wintertime searches for herminiines, hadenines, noctuines, and others that overwinter as half-grown caterpillars will be less productive, so set your expectations accordingly. Watch for feculae. The feeding damage of

■ Burlap bands are a good means to sample late instars of bark-resting owlets, especially on smooth-barked trees that offer few comparable refugia. ■

herminiines is characteristic. Begin looking in the transition zone between the dry upper surface litter and the wet, darkened leaves that are decomposing. We do not know if Berlese funnels and Winkler traps are efficient at extracting caterpillars from soil and litter, but our impression is that neither works well, perhaps because moth caterpillars are adapted to periods of dryness and thus are not easily driven from their feeding sites. Because herminiines are quick to release their grip and feign death, it might be possible to use a set of coarse screens to sift through leaf litter. Another option would be to sift leaf litter with quarter-inch mesh screening over a bed sheet.

Two additional methods merit comment for grass- and sedge-feeding species as well as other ground dwellers. Rains occasionally flood these habitats, and at such times caterpillars will crawl onto emergent plants. Searching such areas while water levels are high can be rewarding (and fascinating). A final option is to cover low-growing plants overnight with a sheet anchored at the corners, and then after daybreak, inspect the underside of the sheet for adhering caterpillars. For some foodplant specialists, we have had success collecting random shoots of appropriately aged foliage, placing them in a large, clear, plastic bag, and then checking daily for the production of feculae. We obtained eggs and early instars of the Sharp-blotched Nola (*Nola pustulata*) and two *Paectes* in this way. We recommend this method only for small species with rapid development, at locations where adults are known to occur in great numbers, and where random foliage collections will not have an impact on the hostplant population. Sleeving is another option: simply place a net bag over plants likely to be hosting eggs or early instars. Many of the foodplant records reported in this work were obtained serendipitously, i.e., where caterpillars turned up as "contaminants" in sleeves that DFS was using to rear other species.

We have had much success checking plants nearing complete defoliation due to the outbreak of a pest species. Co-occurring caterpillars on denuded plants become concentrated on the remaining leaves, making their presence evident.

If you are searching for caterpillars and encounter large numbers of foliage-gleaning ants (especially *Formica* or *Solenopsis*), be aware that they will have removed most of the larvae before your arrival. High numbers of spiders, lady beetles, and other predators, coincident with seemingly low numbers of caterpillars, is also telling…push on.

When a single species is targeted, study its range, habitat, common foodplants, and phenology before starting your search. Consult literature on related species to direct your effort—congeners will be similar in appearance and many aspects of their life histories will be shared. Make a point to check what is known about related Old World owlets, since the early stages of many European and Japanese owlets are well studied.

Keep in mind that while larger and last instars are more easily observed and photographed and are more likely to garner one's attention, the smaller, early, and middle instars are always more numerous and have the added benefit of sometimes being free of parasitoids. Climbing cutworms and many tree-feeding underwings (*Catocala*) will turn up in beating samples as early instars, but once grown these same caterpillars retreat by day into litter or bark crevices, respectively, where they can be exceedingly difficult to sample.

Beating and Sweeping

The most efficient way to locate owlet caterpillars is to beat; use a stick, pipe, or baseball bat to rap vegetation over a light-colored drop cloth. The handheld beating sheets sold by entomological supply houses are a good investment. An inverted umbrella can be used in a pinch. To beat larger limbs or trees, scale up and use one or more bed sheets as drop cloths. Take along students, friends, or colleagues so that corners of the sheet can be positioned more quickly, moved into awkward positions, and held above patches of poison ivy. If there is appreciable debris on the sheet, after a short time, tip the sheet at an angle steep enough to roll or slide the loose material down to one side of the sheet. Many caterpillars will attach themselves to the fabric and adhere rather than tumble away. Rake your fingers through the debris and watch for any movement (especially of smaller, early instars). Return unwanted caterpillars to the plant from which they were dislodged.

Ecotones such as forest edges and isolated plants usually yield more caterpillars than accessible portions of plants

■ Use of a beating sheet. Smooth, white fabrics are best—these allow one to quickly locate even small, early instar caterpillars. Senior author beating juniper, May 2011. ■

growing in forest interiors or larger stands. Moreover, edges usually have overhanging limbs that lend themselves to beating. Sample one plant species at a time so that you know what to feed your collected larvae, and make sure that your sheet is clean before moving to a second plant species. If possible, avoid windy days because caterpillars hold on to foliage with greater tenacity during such weather, and as a consequence beating will produce fewer numbers of caterpillars (and working with a sheet in wind is difficult).

Sweeping can be employed to collect caterpillars from shrubs and low-growing plants. Take a net with a stiff rim, pass it rapidly through vegetation, and then examine the contents of the net bag; we find it helpful to dump the contents onto a white (beating) sheet. This method is effective for collecting caterpillars from grasses, sedges, forbs, and low heaths.

In both beating and sweeping samples, a fair number of the discovered caterpillars will be in the process of molting and therefore not able to attach to their foodplant securely. Treat molting caterpillars with care—the less they are handled the better. They will need to reattach to something to complete their molt. While most will attach adequately to paper toweling, a leaf, twig, or bark, those that have difficulty can be given silk—DFS keeps pieces of the inner cocoons of Cecropia or Promethea Moths on hand to offer molting caterpillars.

Many caterpillars are best beat or swept after nightfall, such as those that hide in duff (many noctuines), on or under bark (some pinions and many late instar underwings), or off plant on nearby vegetation (some legume-feeding underwings). Lowbush blueberries and other low plants, as a rule, can be expected to yield more caterpillars at night. While flashlights are fine for nocturnal searches, headlamps free up one's hands, and are enormously helpful when sweeping and using a beating sheet at night.

Collecting Adults

The standard for collecting moths is to set up a light trap or sheet. Blacklight, mercury vapor, sunlamp, and other bulbs that emit ultraviolet wavelengths yield the greatest catches, although incandescent and fluorescent lights can also be effective. The small portable blacklights that are sold by biological supply houses are adequate to very good for herminiines, noctuines, and most other owlets, but larger blacklights or mercury vapor lamps are more effective for attracting erebines, xylenines, and others. At sites without electricity, use a generator to power a 175- or 250-watt mercury vapor light. Set up both blacklights and mercury vapor lamps when circumstances allow. Some collectors add sunlamps to their setups. In addition to high ultraviolet output, mercury vapor lights and sunlamps have the added advantage of providing considerable illumination for one to work about the sheet. But this added light is also a disadvantage in that many individuals will settle in the darkness of nearby vegetation. A trick employed by beetle collectors that is seeing increased use by lepidopterists, is to run both blacklights and a mercury vapor light on the same sheet and to disconnect the mercury vapor light once every couple hours for a half hour or more. Moths (and beetles) whose activity was suppressed by bright illumination will frequently reactivate and move to the sheet.

Traps can be run without a killing agent to secure gravid females for egg stock. Add inverted egg cartons so that trapped moths will have places to hide and settle. In the morning, gently "unpack" the catch by slowly turning over the egg cartons and inspecting each cell. We also find it worthwhile to run traps in light rains and on cool nights; enigmatically, gravid females sometimes make up a significant proportion of the catch on such nights.

The standard means for obtaining gravid females is to "run a sheet." A white bed sheet is hung vertically adjacent to a light—the sheet reflects the light and provides a landing platform for attracted insects. Place a second sheet on the ground as a drop cloth to prevent attracted moths from working their way into underlying vegetation. While most collectors use white bed sheets, another option is to use sheer curtain material or screen fabrics so that any light will be visible from both sides of the sheet. Leave a few folds or wrinkles in the sheet and the drop cloth to give incoming moths a place to shelter—some will be reluctant to come to rest in the full illumination of a mercury vapor light; e.g., Garman's Quaker (*Orthosia garmani*) is more likely to secret itself in folds or under the drop cloth than to perch beside a bright bulb.

Moths have particular times of the night when they are active; e.g., some daggers (*Acronicta*) will not appear in number until after midnight and many stalk borers (*Papaipema*) have specific flight times that last about 45 to 90 minutes on a given night. Moths will accumulate at a light through the night; thus predawn visits to the sheet will usually be rewarded with high numbers of both species and individuals. Turn off the light bulbs well before dawn to give the moths time to disperse, before birds arrive to feed on them. It is a good idea to periodically tap nearby vegetation to dislodge moths that have settled away from the sheet. On nights of modest moth activity, we will spend the better part of the evening away from the sheet searching vegetation for caterpillars, returning every half-hour or so to see what new moths have arrived.

Full moons when accompanied by clear skies are unfavorable for light trapping. Many collectors plan their field trips around the new moon. Warm stormy nights, regardless of the moon phase, can be exceptionally good, especially if the storms remain distant or rains are light. Winter (2000) and Covell (2005) supply much useful advice on light trapping.

A more challenging and engaging way to locate female moths is to actively search for them by day or night. The same flowers that host butterflies by day may be frequented by owlets after nightfall. *Apamea*, paints (Cuculliinae), loopers (Plusiinae), and flower moths (Heliothinae) are avid flower visitors. A patch of buttonbush, fireweed, or milkweed in full bloom may yield dozens of moths over the course of an evening. Apricot and chickasaw plum blossoms can be outstanding in the spring. Flower visitation often peaks at twilight or very soon after dark, but of course there are moths that wait until midnight or even dawn to take to the wing. Expect some very good nights, many slow nights, and some with no activity—this is the way with moths.

Walking suitable habitat and inspecting vegetation with a flashlight is a good way to locate moths, especially some of the Apameini and litter moths (Herminiinae). When wearing a headlamp, one can watch for orange eye shine. Many species of underwings (*Catocala*) and grass-feeding hadenines (*Dargida* and *Leucania*) can be found while they are ovipositing on trunks or stems of the foodplants. While light trapping at a sheet, search nearby vegetation; invariably you will locate moths that either ignored your lights completely or settled well away from the sheet. Keep in mind that the moths that arrive at lights tend to be males, whereas those located by searching vegetation will yield a more balanced proportion of females.

Many moths can be found during the day. We have reasonable success flushing moths from open habitats such as beaches, sand plains, and grassy fields. Marshes and other wetlands are also good, especially for renias, zanclognathas, and other litter moths (herminiines). As might be guessed from their bright hindwing coloration, underwings (*Catocala*) can be flushed during the day. Tapping, the preferred method for obtaining female underwings, is discussed on page 99.

Males and females of most owlets take nourishment from the sugary solutions provided by flowers, broken tree limbs, oozing plant wounds, rotting fruits, and accumulations of honeydew excreted by aphids and other homopterans. Tree wounds are attractive to a diversity of moths—any moist bark patch that has an abundance of flies, wasps, and especially butterflies during the day is sure to be a flurry of activity by night. A well-studied tree wound in an aged English oak in New York City's Central Park makes the case: as of this writing some 23 underwing species and dozens of other owlet species have been recorded feeding at the tree (Winn 2008, unpubl. checklist). Over a six-week period beginning in late July, John Peacock (1981) observed hundreds of adult *Catocala* representing 18 species visiting a dying American elm that was oozing sap through entry tunnels bored by scores of elm bark beetles. Black birch and sugar maple sap are attractive to a range of early spring owlets; any broken branch, recent cut, or other wound is bound to draw the attentions of moths and other insects.

Baiting

Sugary plant secretions can be mimicked by concocting fermenting mixtures of sugar, fruit, beer, wine, molasses, etc. The recipes of some of our colleagues border on alchemy. After preparation, which may include a period of aging to allow fermentation, the mixtures can be used to bait owlets. Baiting or "sugaring" is a time-tested technique for sampling owlets, especially erebines, herminiines, xylenines, and a variety of fall migrants (including hadenines, noctuines, condicines, and as nectar starts to wane in late fall, even avid

■ **Moths at beer and brown sugar bait. Above:** A good October baiting night in north central Pennsylvania. Most of the moths are the Bicolored Sallow (*Sunira bicolorago*) and five species of pinions (*Lithophane*). **Above right and right:** Fall-migrating Armyworm (*Mythimna unipuncta*) fueling up. ■

WINE ROPES

Ropes dipped in wine (or bait) will draw an array of owlets and other moths. Tim McCabe uses cheap red or white wine to which he adds sugar until no more will go into solution. In a five-gallon bucket with a secure lid, Jim Wiker pours a pound or two of brown sugar and a dash of amyl acetate (banana oil) into two to three gallons of sangria. Ropes made of cotton, hemp, or jute are then immersed in the mixture and hung from limbs or strung between two sticks in treeless landscapes. Wiker's wine bucket contains more than a hundred 1.5 meter rope sections that he hangs just before dark. You may want to wear rubber or plastic gloves when deploying and retrieving the ropes. Wine ropes work well in the fall and winter for myriad xylenines, many migratory owlets, and various others.

flower visitors such as plusiines). A primary advantage of baiting is the quantity of moths that come on the best nights. Few other methods have the potential to produce hundreds of individuals over the span of an hour's time, and no other method rivals the technique in late fall, winter, and early spring. Moth diversity studies based solely on light samples are often conspicuously deficient in abundant and diverse groups that are easily sampled at bait. Baiting is an effective method for obtaining females because bait catches are much less male biased than light-trap catches. The main disadvantage of baiting is its unpredictability; many nights the results will fall short of expectations and the resources invested, as discussed below.

Bait concoctions vary from simple to complex (and bizarre) (Holland 1968, Sargent 1976, Winter 2000). Many experienced baiters swear by one ingredient or another like blackstrap molasses or their own, sometimes secret, additives. DFS uses a fairly simple recipe: one can (12 fl. oz.) of cheap beer (or apple cider), 1½ cups sugar, ¼–½ cup molasses, about four overripe bananas (or the equivalent in apples, peaches, pears, or quinces), a brewer's yeast tablet (optional), and a spoonful of cornmeal (optional). The mix is then run through a blender, although hand mixing will suffice. The bait can be used immediately but will work better if allowed to ferment for a few days. Do not store bait in a sealed container—there is a risk it could explode from gas pressure. Good bait should smell strongly of alcohol and yeast. Do not clean the container between batches; just add fresh ingredients to whatever remains. Not surprisingly, fermenting fruits, such as overripe watermelon, also draw moths and sometimes in great numbers (Himmelman 2002: 21). Wine mixtures, used extensively in Europe, are seeing broader use by owlet collectors (see text box above).

Volatile substances that occur naturally in fermenting sugar baits can be used to attract moths (or augment a bait mixture). Foremost among these are isobutanol (2-methyl-1-propanol) and acetic acid (Meagher and Mislevy 2005). Landolt (2000) reported another short-chain alcohol, 3-methyl-1-butanol, as attractive to some erebids and noctuids.

In summer you can apply your bait to tree trunks before sunset. In cooler seasons, if at all possible, apply by noon or even the day before and retouch around the edges about 30 to 60 minutes before dusk. Do not rebait the entire patch. Such prebaiting can make a significant, and sometimes a more than tenfold difference, especially in fall and winter; we have even experienced occasions when trees baited the evening before attracted more moths than our set of newly "painted" trees. In summer the difference between seasoned and fresh bait trails is less, but applying the bait early and retouching along the edges is still a good idea. If trees are in short supply, use wine ropes (see left) strung between two poles or sponges, soaked in bait, and then hung from branches or set in shallow dishes, on plastic lids, or even placed directly on the ground.

While both butterflies and moths that have been imbibing bait for a time will become intoxicated, others are quick to fly off. Approach the bait slowly and keep your flashlight beam off the bait patch (and moths) at first. Once light has been directed on a moth, do not interrupt the beam. Some collectors carry a net in one hand for especially active moths like underwings (*Catocala*) and the Cabbage Palm Caterpillar (*Litoprosopus futilis*). Startled xylenines tend to drop to the ground (into leaf litter) and feign death, so if you are carrying a net place it beneath the bait patch before drawing your headlight beam across the bait patch. Some collectors clear leaves from the base of the tree at the time they apply the bait.

To "paint" tree trunks use a broad, clean brush (8–10 cm) and apply bait in a patch roughly 20–30 cm long at head height. Don't worry about bait dripping down the trunk. Chunks of banana and other fruit in the bait can be mashed against the bark with the brush. To ensure that you are able to locate painted trees, follow a trail, edge, or roadside, or bait areas with relatively little understory. Flagging tape can be used to advantage. Select trees with smooth bark or plates of smooth bark: pines, hickories, cherries, and birches are all good. Corky or absorbent bark (like white oak or cedar) is best avoided. Vary the direction and wind exposure. In cool seasons, be sure to bait sunny portions of the trunk. Most moths will arrive within the first hour or two—this is especially true of winter moths but also for many summer-active taxa, including species that normally do not appear at a light until after midnight.

Baiting is unpredictable, and often there will be no obvious explanation for poor or spectacular results. In our experience, it is most effective in temperate woodlands and forests where bait has analogs in sap flows, tree wounds, and senescing fruits that moths would be visiting regularly. Dry pine and oak woods can be exceptional. In northeastern forests and barrens, one sometimes sees dozens of moths on a single bait patch. On rare occasions you will attract thousands of pinions and sallows (xylenines), or hundreds of underwings and zales. A 200-meter bait trail with 20–40 baited trees in southern New Jersey will yield as many as 40–50 species in a single June evening. By contrast, June can be the worst month for baiting with yields of less than one moth per tree. The efficacy of baiting sometimes drops off in mesic woodlands, deserts, and elsewhere where the natural analogs of bait are either too abundant or too scarce—we often hear colleagues grouse that where they live, the technique is neither worth the time or effort it takes to prepare the bait, nor the waste of a good can of beer. Abundant honeydew, overripe fruit, and nectar availability will depress the effectiveness of bait. In this regard it is important to note that visitations over the winter to spring bait season will drop off abruptly when the first red maples burst into flower. In general, moth numbers at bait during the growing season will not approach those seen during the fall and winter months, with notable exceptions: zales are often exceptionally common in pinelands, as are underwings (*Catocala*) in oak-hickory woodlands. Few entomological experiences rival a good underwing baiting night (see Holland 1968: 146 for a splendid essay about one such evening, presumably in western Pennsylvania).

In late fall, winter, and early spring, warm days over 18° C (64° F) with a mild evening are best; high humidity, light rain, or drizzle can help, especially in xeric habitats that have been dry for some time. Moths will begin arriving before dark, peak during the early evening, and continue to arrive in decreasing numbers until temperatures drop. (On warm and stormy nights moths will remain active all night.) In general, the minimum sunset temperature for good cool-season baiting varies from about 7° C (45° F) in New England to about 10° C (50° F) in southern New Jersey. In summer, temperature is less important and baiting can be good on cool evenings. Baiting is only slightly affected by moon phase. On bright nights trees in the open may yield fewer moths than those in the shadows. In suburban areas it is best to avoid baiting trees that are near lit porches or street lights.

Sugar baits attract more than moths and butterflies. Bears and skunks will lick at a bait patch. White-footed mice may add to the enjoyment of checking a bait line; in the pinelands of New Jersey and southward, one will sometimes encounter a gray fox wrapped around a tree trunk, up on its haunches, licking at bait. Baiting is also a good way to observe flying squirrels; some individuals eat mainly bait, while others will feast on the moths. Finding wings at the base of a bait patch usually indicates a flying squirrel. In winter, eastern screech-owls are occasionally seen hunting a bait trail for moths and mice. Caterpillars, especially climbing cutworms and tiger moths (Arctiinae), also may be found imbibing bait.

Floral scents are attractive to many flower-feeding adults, including armyworms (*Spodoptera*), the Corn Earworm (*Helicoverpa zea*), darts (*Agrotis*), the Velvetbean Caterpillar (*Anticarsia gemmatalis*), *Mocis*, and a range of loopers (Plusiines) (Meagher 2002). Like sugar baits, floral scents tend to attract both sexes. Use caution when working with any such chemicals, as some may prove to be health risks.

JOHN PEACOCK'S BAIT RECIPE

The bait has two basic components: overripe, fermented bananas and a solution of beer, brown sugar, apple juice, grape juice, and molasses. For the banana "base," take 10 or more pounds of peeled, overripe bananas and mash them in a large Tupperware® container, and then let the mush ferment for two or three days in the closed container at warm temperatures. Occasionally stir the mixture during the first two days. Decant and discard any liquid that accumulates.

Prepare the solution that will be added to the fermented banana base as follows. In a 5-gallon pail, mix 48 oz. of red grape juice, 32 oz. of apple juice, 10 lbs. of dark brown sugar, 5 bottles of beer, and 16 oz. of "robust" molasses. (Avoid ingredients with preservatives.) Keep the pail loosely covered and at warm temperatures for three weeks or more prior to use, stirring every few days to be sure all of the sugar is dissolved.

Prior to use, stir in a few cups of the above liquid mixture to the banana base, and then spoon the resulting banana/liquid mixture into a round, flat plastic bait pan, and place in the trap. The bait will improve after a few days in the field. When humidity is low, add some of the liquid mixture to the bait every other day or so to keep the bait adequately moist. Also, check to be sure visiting moths haven't imbibed all the free liquids; this sometimes happen on nights with elevated activity.

It is best if the bait is a little "tacky" so that there is a substrate on which the moths can rest while feeding. You may use the same starting bait over a three- to five-week period, adding a spoonful or so of the fermented bananas and a little of the liquid mixture from time to time. After using the bait repeatedly, it may appear "caramelized," but will still be effective.

Bait Trapping

An alternative to painting bait on tree trunks is to employ bait traps. Traps require less maintenance and attention and often yield splendid catches of owlets, as well as nymphalid butterflies, hawk moths, and other insect life. Bait traps have other advantages: they run all night and they can be tied to a cord and pulled high into (canopy) trees, or placed in localities that would be inconvenient or inaccessible for running a bait line. Additionally, they can be placed out at any time and picked up well after sunrise or even a day or two later (although with standard trap designs many moths will manage to find an egress from the trap after daybreak). Initially, you may want to run a trap in your yard over the course of a few weeks or months to get a handle on your local fauna and to develop a bait and routine that works well for you. We venture that you will find the experience engaging and rewarding, and at the very least will see owlets and other insects that you would rarely encounter otherwise.

While the same bait concoctions noted above can be poured into a pan in your bait trap, we recommend using a more solid bait, e.g., a mash of a half-dozen or more overripe bananas over which liquid bait is poured to encourage further fermentation. (We share John Peacock's proven recipe—fine-tuned and field-tested for underwings (*Catocala*)—on the previous page). Leroy Koehn makes an apple-peach bait by combining a cup of sliced apples, an equal measure of sliced peaches, and a cup of sugar in a plastic bag; he then keeps his "ambrosia" until it starts to ferment. In traps, semi-solid baits prevent drowning of insect visitors, remain active over longer periods, and are easier to service. Over warm and dry periods, mash baits will need to be rehydrated, often in late afternoon or early evening, with more liquid bait, water, or as is sometimes used by Weston Henry, a mixture of ethanol and water.

The most common bait trap design has a narrow entry area near the bottom where bait is positioned and a large upper screened area that collects moths that have finished feeding. Traps range from less than 25 cm in diameter to large, 75 cm diameter constructions that can easily retain 100 or more underwings. A band of dark fabric around the top will encourage settling, and consequently ensure better catches. Some collectors add a few leaves, or halved or quartered egg cartons at the bottom of the trap to provide sheltering nooks to visiting moths. It is best to service traps an hour or so before daybreak. Such predawn checks work for underwings, litter moths (Herminiinae), and most other owlets. Xylenines, and other winter moths are more adept at finding their way out of traps after they have fed; check your traps more frequently, especially in early evening when activity is at its peak. To discourage visits from flies and hornets, cover the bait pan during the day (leaving it in the trap), and then uncover the bait an hour or so before dusk. See Winter (2000) for additional information on bait trapping.

■ Catches in bait traps can be prolific (and interesting) and, just as often, disappointing, even over the span of just a few days—see text. ■

Collecting, Vouchering, and Conservation

Much remains to be learned about the life histories of eastern owlets, so much so that even the weekend biologist or student can expect to make worthwhile contributions to our knowledge of this extraordinarily diverse group of moths. As you read through this book, taxonomic problems and uncertainties about the foodplants and life cycles will surface by the dozens. Pick a group and start rearing; take notes, images, and videos; save appropriate voucher specimens.

Larval, pupal, and adult vouchers that are well preserved and labeled will become a scientific legacy. They can be examined and reexamined, redetermined, dissected, or their DNA can be sequenced. An obvious case for the importance of vouchers is seen when a species proves to be more than one entity. Many eastern litter moths (Herminiinae) are proving to be complexes of two or more biological species. 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. Many future possibilities will be limited only by the lack of preserved specimens. Our collections will be our longest legacy, attesting to times, locales, and climates of the recent past.

We are advocates of collecting and life history studies. These activities are 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. Many of today's most active insect conservationists and researchers were first collectors (Wagner 2007e). The National Wildlife Refuge System in this country was established by funds generated by duck stamps purchased by bird hunters. Collecting efforts must be carried out in an ethical and responsible fashion. The Lepidopterists' Society statement on collecting (http://www.lepsoc.org/statement_on_collecting.php) should be read and followed, regardless of whether the intent is to release or voucher the reared adults (and reared adults should be released only near their place of origin and during their natural flight season when they are more likely to reproduce successfully). Never remove more than a fraction (about 5–10%) of the number of individuals you believe to be present in a population. Species with conspicuous caterpillars or those that are otherwise easily collected—for example, many stalk borers (*Papaipema*) and flower-feeding flower moths (Heliothinae)—could easily be affected as a result of a single overzealous collecting effort. If one were to collect the visible host flowers in a small *Schinia* colony, a population could be seriously diminished. Be especially careful if the foodplant is highly localized or scarce. When appropriate obtain and carry (necessary) permissions and permits.

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 taxa might be declining, understand a species' biological requirements, or develop management practices for an imperiled colony. Outside of the Northeast and upper Midwest comparatively few moths receive legal protection, are considered in management practices, or are used in conservation planning, simply because we know too little about them.

Numerous aspects of the life history may be learned by collecting, rearing, and observing caterpillars: e.g., the number of annual broods, seasonal and daily activity patterns, and cocooning and overwintering behaviors. Hostplant-use patterns, and how these vary geographically, are remarkably incomplete for most of the species in this guide. Such knowledge is critical in the design of management plans for species of conservation interest. We desperately need collections documenting the impacts of introduced biological control agents on native caterpillars. Should you engage in appreciable rearing, an exercise which we find intellectually rewarding, as did Douglas Ferguson and John Franclemont to whom this book is dedicated, remember that an important part of this process is good record keeping. Save and label any parasitoids, and above all, share your findings. A useful reference for handling and preparing specimen vouchers is Winter's (2000) *Basic Techniques for Observing and Studying Moths and Butterflies*.

Feeding Adults

To be kept alive, adult owlets should be fed daily or every other day with sugary solutions. The exact proportions are not important. A two- to five-part water to honey mixture or maple syrup solution will work fine, but table sugar or almost any other sweet may be used. More dilute mixtures are acceptable—adults will simply imbibe more and secrete the excess water. We offer a solution in a saturated cotton ball, small squares of sponge, or a tiny wad of toilet paper. Fruit juices and small slices of fruit, e.g., moistened apples and grapes, also can be offered. Change fruit pieces after a day or two, because they soon spoil. We travel with raisins; small sections are cut, soaked, and placed where the females will have easy access. Sport drinks are eagerly accepted by a gamut of Lepidoptera—we sometimes add Gatorade® or Powerade® to the food of long-lived underwings (*Catocala*) and zales. Wine will also serve. If egg number is important, try adding a trace of egg white to the solution to enrich the diet.

Obtaining Pairings

With few exceptions, field-collected females already will have mated. Pinions and sallows that overwinter as adults do not mate until late winter or spring. To obtain pairings, place one female and two or three males in a spacious container with a screen or mesh cover that will allow good air flow (for circulation of courtship pheromones). All moths should be well fed. Although mating may occur soon after the sexes are placed together, expect the majority to delay pairing—many moths are reproductively active for specific periods during the night. Generally, mating pairs will stay together for at least an hour, although some species remain coupled until nightfall of the following day.

Obtaining and Handling Eggs

Most owlets oviposit readily in captivity. Female owlets can be expected to produce between about 300 and 1500 eggs if kept well fed, although conifer feeders and owlets that feed on hardened summer foliage produce fewer, larger eggs. Some moths (e.g., sallows in the genus *Eupsilia*) require multiple matings if they are to continue producing viable eggs.

Place gravid females in small vials and jars. Hang a strip of paper towel vertically, usually with one end draped over the lip of the jar and with the other end bent across the bottom. A minute drop of water can be added to the strip, especially if no food is provided initially. (No free water should be visible.) Most species will lay their eggs on the paper strip, others will lay on the container walls and lid, and some (including many noctuines) will drop their eggs about the bottom of the container. If you believe the species oviposits in cracks or crevices in bark or about buds, add a tightly rolled piece of paper towel or strip of corrugated cardboard into which the female can insert her eggs. A long-pointed abdomen usually indicates that a species positions its eggs in soil or deep crevices. For example, female darts in the genus *Euxoa* oviposit into sand or soil. (If the sand placed in a container has already been screened with fine mesh, you can rescreen the sand to recover any eggs.) Underwings (*Catocala*) and others oviposit in bark crevices—offer these a strip of bark of a preferred host (see also page 100). Lash-eyed sallows (psaphidines) and a few other owlets active in fall, winter, and spring should be held with a twig of their foodplant, with terminal buds, and a paper towel strip. In addition, we sometimes add a piece of dead leaf of a favored host. Grass feeders such as wainscots (*Leucania*) and related genera prefer to oviposit in the leaf sheaths around grass stems—include dried, dead stems in the vial. Daggers (*Acronicta*) prefer to oviposit on smooth surfaces, so hold gravid females in clean, smooth plastic containers or glass jars.

Most owlets require food (see Feeding Adults, above). Sugar solutions can be supplied on a small bit of cotton (less than 5 mm in diameter) placed at the bottom or top of the jar—but not in contact with the paper strip. Punch two or three small air holes into the lid and place the container outdoors, on the north side of your house or on a shady porch. Most species will oviposit one to three nights after their first meal. Some Lepidoptera require elevated temperatures and light to stimulate egg-laying behaviors. Such seems to be the case for many diurnal moths (e.g., many chocolates, *Argyrostrotis*). Females held in vials and jars without foliage, for example those in transport between field and lab, will often lay if they are exposed to elevated temperatures (32–34° C or 90–95° F) for an hour or two.

■ Noctuid eggs range from hemispherical to flattened with intricate surface ornamentation. The clear chorions of the Reddish Speckled Dart (*Cerastis tenebrifera*) eggs are all that remain after hatching. Dark eggs in the image contain first instars that failed to eclose. ■

A reliable means of securing eggs is to sleeve females on an appropriate host. Females should be fed before they are introduced into the netting. Alternatively, add a saucer of fruit (such as crushed grapes), or place a plug of cotton saturated with honey or sugar water inside the sleeve or on top of the sleeve, positioned so that the female can feed through the bag.

DFS places conifer feeders in a clean ice cream carton, plastic box, or widemouthed glass jar of at least a half-gallon capacity. He adds a sprig of the foodplant, with new growth if available, so that the upper needles touch the cover. The container is then covered with nylon netting or other airy cloth. Finally, he adds a feeding plug, placing it inside the container or simply setting it upon the netting cover. Each evening the containers are slightly moistened (misted). Feeding plugs are changed every two or three nights. Conifer foliage held in a vase or florist water pick will last ten or more days, and sometimes long enough for the eggs to hatch and the first instars to establish.

Newly laid eggs are often cream in color but may turn yellow, orange, pink, red, or gray within a day. Infertile eggs often fail to change color and/or collapse. Typically noctuoid ova are hemispherical with lacelike ribbing. Some are handsomely banded. A day or so before hatch, the eggs may darken, in large measure because the developing caterpillar becomes increasingly visible. The chorion, or egg shell, is translucent in nearly all noctuoids; hatched eggs of the Reddish Speckled Dart, *Cerastis tenebrifera*, are shown in the photograph to left.

Hatching rates are generally better if the eggs experience natural humidity in well-ventilated containers. Eggs laid on flowers or leaves quickly mold if left in sealed containers. Adding leaves to vials, even when the ova are on the verge of eclosion, may prevent hatch in sallows, pinions, and others. The volatiles from cut pine foliage also are purported to depress hatching rates—here again, ventilated containers are recommended. If eggs normally hatch within four to ten days, no watering is needed, although a light misting may be helpful under dry conditions. Be sure that the ova then have time to air-dry if they are to be housed in an airtight container.

For eggs laid in the fall (e.g., most Xylenini) minimal care is needed. Keep the eggs in a shady outdoor place in a small jar with a tight, but not completely sealed, lid. Egg jars need protection from direct sun and from heavy precipitation. Air holes are optional—they provide ventilation and regulate moisture, but can be a liability in that they make a container subject to flooding and provide a means of escape for newly hatched caterpillars. While a garage or enclosed porch prevents flooding, discourages predation, and moderates cold winter temperatures, be forewarned that eggs held there may hatch before food is available in spring. Eggs that overwinter on trees and shrubs are adapted to swings of heat and cold, and unless the stock comes from a much warmer climate than where you live, the ova will not need protection from extreme temperatures. Periodic mistings will prevent desiccation, but make sure the eggs are air-dried afterwards. The greater danger will be the growth of mold because the tendency will be to supply considerably more moisture than is needed. John Peacock overwinters eggs in his garage but, come March, he transfers the eggs to an airtight plastic container with a slight bit of moisture; he places this in his refrigerator to prevent early hatching. As appropriate foliage becomes available, he removes the eggs. This strategy has two other advantages: it allows one to stagger cohorts of larvae, starting some early and some late, and more importantly, egg hatch can be timed around one's travel plans.

Many lepidopterists sleeve their eggs for ease of handling and to avoid the uncertainties surrounding moisture management. If females normally oviposit directly on leaves, position the eggs so that they are adjacent to suitable food: e.g., eggs laid on paper strips can be cut away and stapled to the underside of host leaves. While sunny twigs are generally best, branches that experience long periods of full midday sun, with temperatures exceeding 32° C (90° F), are best avoided. If the caterpillars are active and normally have to disperse to find food, e.g., underwings (*Catocala*), and many pinions and sallows (both Xylenini), one can simply place the eggs in the sleeve. However, for most owlets, early instar survival will be enhanced if neonates are started in vials, and later introduced into sleeves as late first to third instars.

Rearing Caterpillars

Owlet caterpillars are easily reared if provisioned with fresh foliage, their containers are kept clean, and they are offered suitable pupation substrates. Monitor both growth and feculae production daily; most species will show visible growth over any one- to two-day window. Only during a molt, and prior to pupation, should feeding slow down. If growth rate or feculae production falls off (and the caterpillar is not approaching or coming out of a molt) consider trying foliage of a different age or species.

There is no single best method—or stated differently, no two lepidopterists use the same rearing methods. Much advice on rearing caterpillars appears in Wagner et al. (2002) and Wagner (2005), and Todd Stout's website on raising butterflies is loaded with terrific information about caterpillar husbandry (http://www.raisingbutterflies.org). Rather than repeat information found in these places or other widely available works (e.g., Winter 2000 and Covell 2005), we address a few points and offer suggestions geared toward the rearing of owlet caterpillars.

Most spring and summer species will complete their development quickly, within four to five weeks. Conversely, those that overwinter as larvae may spend eight to ten months in this stage. Because owlets are largely nocturnal, it is often possible to speed development by rearing them in darkness or at least by minimizing the number of hours that they are exposed to light.

As a group, owlets are reasonably hardy and can be reared at moderate densities. Some ventilation will enhance survival, especially if multiple caterpillars are being reared in a single container, but it is more crucial that foliage remain fresh. Rare, desirable, or cannibalistic caterpillars are best reared individually to aid study, diminish the spread of disease, and circumvent cannibalism. Also, if data on parasitoids are desired, it is best to raise each caterpillar in its own container.

Neonates will imbibe water. Access to water is especially important if the caterpillars have hatched and wandered without encountering food. As a matter of routine, we lightly mist newborn larvae either before or immediately after their transfer to host foliage. Lethargic caterpillars, e.g., *Paectes*, are best picked up individually with a needle or fine brush (e.g., a #1 camel hair, pointed artist brush), and placed onto appropriate foliage. More mobile caterpillars, e.g., underwings (*Catocala*) and various other erebines, easily find their way onto suitable host tissues.

Many spring-active noctuids can be reared on young cherry or walnut foliage. Other hosts that are accepted by a large fraction of temperate caterpillars include alder, apple, basswood, birch, blueberry, and oak. Plants that continue to produce young leaves late into the spring or early summer such as alder, birch, cherry, walnut, and willow will allow one to supply new foliage long after oaks and hickories have hardened for the summer.

Noctuines include many generalists on nonwoody plants and will accept a range of forbs and grasses. Most will find something suitable in a salad of fleabane, clover, dandelion, and grasses. Organically grown lettuce or the inner leaves on non-organic heads are options, even in the winter months; romaine and other leafy varieties are presumably more nutritious, and less likely to cause diarrhea. Many owlets can be reared on artificial diets such as those sold by biological supply houses. BioServe® makes dozens of diets for a wide range of insects. Bergomaz and Boppré (1986) describe a diet made from beans that is acceptable to a variety of noctuoids. Tim McCabe has successfully reared a variety of erebids and noctuids on BioServe's pinto bean diet; he occasionally makes customized batches for foodplant specialists by drying leaves of the hostplant, and adding ground up leaves to the diet before it is poured into diet cups. Many borers will accept carrot, potato, and sweet potato: core out a hole about the same diameter as the caterpillar and then introduce the larva head first; sometimes it helps to then seal the hole with a plug or to position the entrance such that the caterpillar cannot easily back out.

Vases and floral water picks can be used to great advantage in open-air containers and other situations in which the foliage would wilt within a few hours. The Oasis® foam sold by flower shops can be purchased in bricks and cut to size to keep foliage fresh for days. Grasses and many forbs often do not hold up well once they have been cut—consider potting these and then covering the foodplant (and larvae) with netting.

Many owlets require a layer of soil or peat in which to pupate. Failure to provide an appropriately moistened pupation substrate is probably the most common cause of mortality in reared owlet prepupae and pupae. A deep layer (5 cm or more) (2 in.) of lightly moistened peat, potting soil, or dirt should be offered to any caterpillar that wanders for extended periods, especially if the caterpillar is showing no interest in eating or otherwise appears to be prepupal. We use peat for all univoltine, spring-active caterpillars. Many balsas (balsines), brothers (dilobines), dagger moths (acronictines), and foresters (agaristines) fashion their pupal chambers in wood. Offer them chunks of soft pulpy wood, e.g., fallen branches and trunks with wood that is light and soft.

Sleeving

Fine mesh bags or sleeves can be used to enclose females for oviposition or for rearing cohorts of larvae outdoors. In addition to being the most time- and labor-efficient means of rearing caterpillars, sleeving has other advantages: the larvae are less susceptible to stunting, caterpillars can be left unattended for a week or more, and, because sleeves are well ventilated, diseases are rare. Finally, the sleeved caterpillars are exposed to normal photoperiods and temperatures, and consequently will be synchronized with native populations.

Make sure to vigorously shake or rap any branches that are to be sleeved in order to dislodge ants, spiders, lacewing larvae, assassin bugs, ladybugs, and other natural enemies. Predaceous stink bugs often accumulate on the outside of sleeves and feed on the enclosed caterpillars through the netting. Upon occasion a bird will peck through a sleeve to feed on the occupants; hornets or wasps may also chew through and raid the sleeve. Valuable livestock can be protected from both by double sleeving or using hardware cloth. Pillowcases, because they are made of denser fabric and are nearly opaque, offer more protection. Small sleeves must be moved frequently; larger sleeves have the advantage of being low maintenance.

■ Sleeves of fine netting or fabric, such as the five-gallon paint filter bag used here, have many advantages over container rearing—see text. ■

Prepupal larvae of most owlets, especially those that pupate in soil or wood, should be removed from the sleeve at least every other day and placed over peat or other suitable substrate; left untended, some will chew their way through the sleeve in an effort to locate a suitable pupation site (or die of dehydration and exhaustion). Other species will cut bits of the sleeve for use in the walls of their cocoon. If you know the species pupates in wood, this can be added to the sleeve. A safe option is to periodically harvest nearly mature larvae from the sleeve and rear them indoors for the last few days.

Sleeves may be purchased from biological houses or made by hand. We have made large sleeves for enclosing entire branches from synthetic tent screening fabrics. The one- and five-gallon paint filter bags sold at home improvement stores are economical and handy for rearing small larval cohorts. Pillow cases can be purchased used from secondhand stores or at flea markets. When necessary, or in case of disease problems, launder sleeves with ordinary detergent and some added chlorine bleach.

Overwintering Larvae and Pupae

Our general suggestions for overwintering stages undergoing diapause are given in Wagner (2005). We recommend that rearing lots be held outdoors in garages, sheds, or porches, where they will be exposed to normal temperatures, humidities, and photoperiods. Those who live in the North must take measures to protect their livestock from subfreezing temperatures—prolonged exposure to temperatures below about −3° F (26° C) can be fatal, especially for larvae or pupae that are usually underground or sheltered near the ground under leaves. DLW overwinters collections in a garage, periodically misting the lots through the winter. DFS, who lives in coastal New Jersey, simply places his pupal containers in foam coolers packed with dry leaves, and places the coolers in a shady, sheltered spot outdoors, e.g., an outside porch or crawl space that stays above −3° C (26° F). Another option is to cover the rearing vials with fabric or a lid with several holes, place them on a tray or in a cage, and set them into a shallow pit so that they are elevated just above the ground. Then cover the vials with a deep layer of leaves. Either invert the vials so they do not fill with water or lay a sheet of plastic or wood over the top before covering them with leaves. We have lost collections to mice—take measures to safeguard your lots. In most years, we bring our collections indoors in February or March to accelerate emergence so that we have more time to work with emerging adults, in advance of the field season.

Owlets that overwinter as caterpillars may feed intermittently during periods of mild weather: included are many darts (Noctuini), litter moths (Herminiinae), and some arches (Hadenini). Winter-active caterpillars eat fallen leaves or are general feeders on forbs and/or grasses. A method with which we have had much success is to place the livestock in a clay flowerpot partially filled with soil and a few layers of food leaves. The pot is then covered with screening or muslin and partially buried outdoors, exposed to normal rainfall, snow cover, and temperatures. When especially heavy rains are expected, we temporarily cover exposed pots under a sheet of wood or plastic.

Natural Enemies

Caterpillars are attacked by a menagerie of pathogens, parasites, parasitoids, and predators. Soil-dwelling species are susceptible to attack by *Beauveria*, *Cordyceps*, *Metarrhizium*, and other entomophagous fungi. Owlet larvae also fall victim to protozoan and nematode parasites. In the southern Appalachians, our spring caterpillar collections often yield a mermithid nematode (Parasitoids Plate, row 1, left); quakers (*Orthosia*), pinions (*Lithophane*), and other spring xylenines are among the most common casualties.

The early stages of owlet moths host a variety of hymenopteran (wasp) and dipteran (fly) parasitoids. These attacks are usually fatal; and hence, from an ecological viewpoint these enemies function as predators. For this reason, entomologists refer to them collectively as parasitoids (as opposed to parasites, which often do not kill their hosts). Parasitoids that immediately arrest the development of their host are **idiobionts**; many egg and pupal parasites are in this category. **Koinobiont** parasitoids allow their host to feed and develop. Koinobionts may begin feeding as soon as they hatch from their egg, or delay development until their host reaches a certain instar, stage, or size. In univoltine species, koinobionts may diapause for months before commencing their own growth. Most parasitoids grow slowly at first, consuming only blood (hemolymph), their own nutritive cells released into the host, and/or nonvital host cells and tissues, then finish off the host in a burst of feeding and growth, often triggered by the host larva's size or hormonal state. A common strategy is to wait until the host larva has spun its cocoon or constructed a pupal cell (and thus fashioned a safe haven for the parasitoid), before consuming the prepupa. While the vast majority of the parasitoids attacking owlets are **endoparasitoids**, developing within the body of their host, a few such as *Euplectrus* (Eulophidae), are **ectoparasitoids** that live affixed to the outside of the host's body (Parasitoids Plate, row 2). Owlet larvae fall victim to a diversity of braconids, ichneumonids, encyrtids, eulophids, and numerous other families of parasitic wasps. The third volume of Krombein et al. (1979) includes a host index with dozens of records for hymenopteran parasitoids.

All early stages are attacked. Owlet eggs are parasitized by minute mymarid, scelionid, and trichogrammatid wasps. Minute microhymenopteran wasps—eulophids, encyrtids, among others—attack first or second instars. The importance of such early mortality factors is underappreciated, and we confess that much of our treatment below pertains to the parasitoids one is likely to rear out from collections of late instar owlets.

Two microhymenopteran lineages that issue from late instars are worthy of special mention because of their widespread prevalence. *Euplectrus* and related eulophids can be very common, especially in the South: once fully fed, the larvae crawl beneath the vanquished host and spin a series of dirty white to brown cocoons. The blackened cadaver with its array of cocoons appears to be enveloped by fungus—no doubt, a biological ruse that affords the wasp pupae protection. Polyembryonic encyrtids parasitize many loopers (Plusiinae)—a single egg laid by the female wasp will divide mitotically to yield more than two thousand genetically identical sisters (Strand 1989, Ode and Strand 1995). The whole of the looper's body will become packed with minute encyrtid larvae and ultimately with the pupae (Parasitoids Plate, row 1, center).

Three braconid subfamilies are reared from owlet larvae with regularity: Microgastrinae, Meteorinae, and Rogadinae. At maturity, microgastrines bore out through the body wall and spin small, yellow to white, oval to barrel-shaped cocoons, usually with loose silk over the exterior, on or near

■ **Tachinid Flies.**
Row 1: Three tachinid (macrotype) eggs on *Lithophane petulca* (left); white arrow points to breathing tube of tachinid inside body of *Eucirroedia pampina* (center); tachinid maggot just issuing from cadaver of *Orthosia hibisci* (right).
Row 2: Larva and newly forming puparia of *Voria ruralis* in cadaver of *Autographa metallica* (left); tachinid puparium adjacent to (euclidiine) caterpillar host (note necrotic hole from where the larva issued) (center); nearly a dozen tachinid puparia alongside the cadaver of their vanquished *Acronicta increta* host (right). ■

the victimized larva (Parasitoids Plate, row 5). Gregarious microgastrines may issue from the larva in groups of a dozen or more (Parasitoids Plate, rows 4 and 5). More commonly, and especially in the spring, you will encounter solitary microgastrines attacking early to middle instar daggers (Acronictinae), hairy-eyed owlets (Hadenini and Orthosiini), and pinions, sallows, and kin (Xylenini). Upon emerging from the host caterpillar, prepupal *Meteorus* larvae drop down on a strand of silk and then spin a hanging, often structurally diagnostic cocoon (Parasitoids Plate, row 6, left). Some *Meteorus* have the ability to snap their cocoons about in a fashion analogous to a jumping bean. Rogadine braconids mummify their victims, pupating within their cadavers (Parasitoids Plate, row 3). Most are solitary wasps that issue from middle instars, although one common eastern *Aleiodes* is gregarious and emerges from final instar hosts in number (Parasitoids Plate, row 3, right). Shaw (2006) illustrates the common eastern rogadines that attack owlets.

Many Ichneumonidae parasitize Lepidoptera.[3] Some, such as the Pimplinae, Cryptinae, and Ichneumoninae, seek out, sting and paralyze, and oviposit onto or into the pupae or the cocooned prepupae of moths. The wasp larva develops by consuming its immotile food resource (i.e., as idiobionts). Some ichneumonine oviposit into the final instar while it is seeking a pupation retreat, and delay their own development until the host caterpillar has constructed its cocoon and/or molted into the pupal stage (i.e., as koinobionts). The habit of attacking a caterpillar and then allowing it to complete its larval development (koinobiosis) is common in a number of ichneumonid subfamilies, including the very diverse and

[3] Text for the Ichneumonidae was contributed by Ian Gauld in May 2006.

OPPOSITE
■ **Parasitoids.**
Row 1: Nematode from *Lithophane joannis* (left); *Trichoplusia ni* attacked by *Copidosoma*, a polyembryonic encyrtid (center); eulophid larvae on *Oligocentria lignicolor* (Family Notodontidae) (right).
Row 2: Eulophid pupae on same *Oligocentria lignicolor* (Family Notodontidae) (left); *Euplectrus* larvae on *Spodoptera ornithogalli* (center); *Euplectrus* cocoons on same *Spodoptera ornithogalli* caterpillar-cadaver (right).
Row 3: All *Aleiodes* mummies (Family Braconidae): *A. nolophanae* on *Hypena* (left); *A. quebecensis* on *Acronicta* sp. (center); *A. stigmator* on *Acronicta americana* (right).
Row 4: All microgastrines (Braconidae) on *Condica*: Larvae exiting *C. albigera* (left); cocoon bundles of same braconid on *C. albigera* (center); cocoon bundle and the host, *C. videns* (right) (image from Valerie Bugh).
Row 5: All microgastrines (Braconidae): Cocoon on *Orthosia hibisci* (left); cocoons on *Catocala badia* (center); cocoon bundle on *Mythimna unipuncta* (right).
Row 6: *Meteorus* cocoon from *Spragueia jaguaralis* (left); campoplegine (Ichneumonidae) cocoon on unidentified noctuoid (center); campoplegine (Ichneumonidae) cocoon on *Phyprosopus callitrichoides* (right). ■

■ **Predators:**
Row 1: Bark spider (Thomisidae) (left); three *Photuris* (Lampyridae) larvae consuming pyralid caterpillar (center); *Podisus* stinkbug (Pentatomidae) attacking larva of *Orthosia hibisci* (right).
Row 2: Assassin bug (Reduviidae) feeding on erebine (left); *Zelus* (Reduviidae) feeding on erebine (center); *Podisus* stinkbug (Pentatomidae) feeding on *Coxina cinctipalpis* (right).
Row 3: Ants (Formicidae) consuming caterpillar of *Spodoptera frugiperda* (left); *Ammophila* (Sphecidae) carrying away paralyzed larva of *Panopoda rufimargo* to be entombed in an underground brood cell, where it will be slowly consumed by the *Ammophila* wasp's larva (center). ■

frequently encountered Campopleginae, Banchinae, Cremastinae, Anomaloninae, and Ophioninae. In almost all cases, the parasitoid larva begins feeding in the host caterpillar and then suspends its own development until the host has sought out a pupation retreat; the parasitoid's development is then reactivated, the host caterpillar is consumed, and the wasp spins its own cocoon. Species of Anomaloninae are unusual in delaying development until after the host has pupated. Only among some of the Campopleginae is the host caterpillar killed before it has found a pupation retreat; many spin a black and white mottled cocoon that resembles a bird dropping (Parasitoids Plate, row 6, right) suspended from vegetation by a thread, concealed beneath the cadaver of the host caterpillar, or secreted within the mummified remains of the host. The majority of endoparasitic braconid and ichneumonid wasps attack exposed, externally feeding caterpillars, and consequently tend to have short ovipositors. While most are diurnal, some, such as *Ophion* and *Enicospilus* (Ophioninae), search for hosts at night. A few Banchinae, Campopleginae, and Cremastinae have long ovipositors that they use to probe for concealed hosts, such as those under bracts, in shelters, or boring inside shoots and stems. Although the overwhelming majority of koinobiontic Ichneumonidae are endoparasitic, one common group of Tryphoninae are ectoparasitic koinobionts. These sting the host caterpillar and then attach a black egg externally by a short stalk that is usually placed just behind the host's head—positioned so that the host caterpillar cannot chew through and destroy the egg. The solitary wasp larva develops externally. Summaries of ichneumonid biologies can be found by visiting the Genera Ichneumonorum Nearcticae pages posted on the American Entomological Institute's website (www.amentinst.org).

Tachinid flies, primarily in the subfamilies Tachininae and Exoristinae and to a lesser extent in the Dexiinae, are among

EXOTIC BIOLOGICAL CONTROL AGENTS

It is common practice to release parasitoids and predators from other countries to control introduced pests that have established in our forests and croplands without their normal complement of natural enemies. More than 300 exotic parasitoids have been introduced into North America in the past hundred years to control pest species (Hawkins and Marino 1997). In their compilation, Hawkins and Marino noted more than 50 instances where such exotic parasitoids have been reared from native, nontarget hosts. One example receiving much attention in the East involves the tachinid fly (*Compsilura concinnata*) (right), which was introduced from Europe to control two lymantriine tussock moths: the Gypsy Moth (*Lymantria dispar*) and the Browntail Moth (*Euproctis chrysorrhoea*). The tachinid fly is credited with virtually eradicating the latter (Elkington et al. 2006). In addition to these two introduced pests, the fly parasitoid is known to attack more than 180 native species of Lepidoptera from more than a dozen families, including many noctuoids (Webber and Schaffner 1926, Schaffner and Griswold 1934, Schaffner 1959, Arnaud 1978, Clausen 1978). During Gypsy Moth outbreaks, *Compsilura* densities sometimes reach 10,000 adult flies per hectare (William et al. 1992). Because Gypsy Moths are only present for the fly's spring generation, the fly's second, third, and fourth generations must seek out and parasitize native caterpillars. Boettner et al. (2000) demonstrated staggeringly high mortality rates from *Compsilura* in field trials of two native giant silk moths in Massachusetts. There is growing concern that *Compsilura* and other introduced parasitoids are responsible for the widespread decline of silk moth (Saturniidae) populations across many areas of the northeastern United States (Howarth 1991, Boettner et al. 2000, Kellogg et al. 2003, Elkinton and Boettner 2004). In addition to several species of saturniids, it is our impression that some hawk moths (Sphingidae) and datanas (Notodontidae) are not as common as they were four decades ago in the Northeast (see discussion in Schweitzer et al. 2011). The recent declines of some butterflies, e.g., *Chlosyne harrisii* and *C. nycteis*, also remain unexplained (Wagner 2007d). Among the taxa treated in this volume, the mysterious declines of three *Acronicta* from large parts of the Northeast—Barrens Dagger, Paddle Dagger, Witch Hazel Dagger (*A. albarufa, A. funeralis,* and *A. hamamelis*, respectively), and the Zebra Arches (*Melanchra picta*)—may relate to changes in their natural enemy complexes. In sum, the impacts of introduced biological control agents on native species are in critical need of study and assessment.

the most commonly reared parasitoids of owlets in eastern North America. All are endoparasitic koinobionts. Most tachinids, especially the exoristines, lay their eggs on the surface of the caterpillar; upon hatching, the first instar maggot burrows through the integument, and into the body of the caterpillar. The smooth, white, oval (macrotype) eggs, commonly seen on caterpillars, belong to tachinids (Tachinid Flies Plate, row 1, left). Ovipositing flies tend to place their eggs near the host larva's head so that the caterpillar will be unable to chew into and destroy the eggs. Hard-shelled macrotype eggs take a few days to develop and may be shed if the caterpillar molts before the fly larvae hatch. More commonly, exoristine eggs are thin-walled; these tend to have shorter incubation periods and hatch soon after they are laid. Other tachinids lay (microtype) eggs by the thousands on leaf surfaces, where they are consumed by feeding caterpillars. These minute eggs hatch within the gut of the host and the neonate fly larvae then tunnel into the host's body. A few tachinids are unusual in possessing a piercing ovipositor that allows the female to insert eggs or larvae directly into the body of the host, e.g., *Eucelatoria* females oviposit into loopers (Plusiinae). About half of our tachinids are solitary (a single maggot develops with a host), and the other half are gregarious, with as many as a dozen individuals issuing from a single host larva (Tachinid Flies Plate, row 2, right). At maturity, the maggots of most tachinids crawl from the cadaver, drop to the ground, work their way into leaf litter, and then pupate within the skin of the last instar maggot, forming a hardened, smooth-walled puparium (Tachinid Flies Plate, row 2 center). Others pupate within the host cadaver (Tachinid Flies Plate, row 2, left). Other lineages delay their development until the host caterpillar has pupated: depending on the species, pupation may occur within the victim's pupal casing or exterior to it, within the host's cocoon or pupal cell. Arnaud's (1978) catalog contains dozens of host records of tachinids reared from moths and other insects. While most tachinids are host specialists, others are generalists—the known hosts of *Compsilura concinnata* include over 200 species of Lepidoptera (many of which are owlets) as well as a few Hymenoptera (Schaffner and Griswold 1934, Arnaud 1978). Stireman et al. (2006) recently reviewed the biology and evolutionary history of this important group of parasitoids.

Parasitism rates generally range between 10% and 25% from collections of wild, late instars, but at times can climb much higher. Attack rates sometimes exceed 75% in collections of stalk borers (*Papaipema*) and paints (*Cucullia*). Note that such rates (from single collection events) represent but a slice of the insect's life cycle and that natural enemies are culling larvae over the entirety of a species' development.

Reared parasitoids should be saved, pinned, and fully labeled, with the identity of the host larva recorded when known. It is also good practice to save associated cocoons, puparia, and mummified hosts. Unhatched puparia and wasp

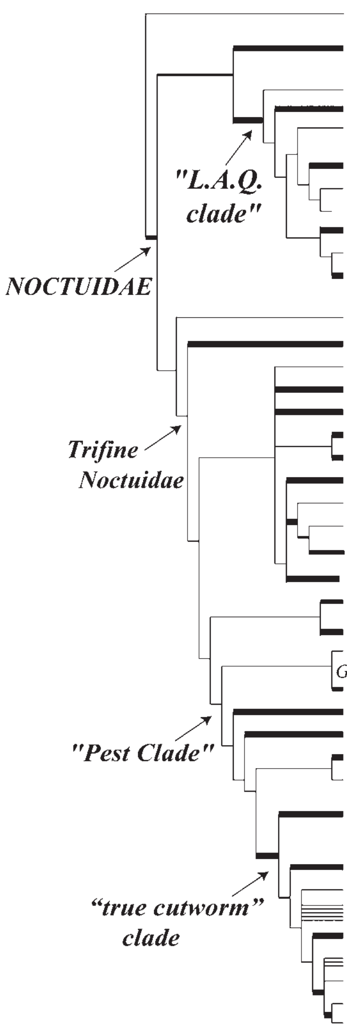
GUEST ESSAY ON OWLET CLASSIFICATION: CHARLES MITTER (UNIVERSITY OF MARYLAND)

Noctuid classification was long dominated by the monumental work of Hampson (1898–1913), despite early recognition of the nonphylogenetic nature of Hampson's arrangement. Over the past 15 years, however, noctuid phylogeny and classification have been under very active study, resulting in continual change as new evidence emerges. The snapshot of current understanding offered here is based on DNA sequence data, from which especially rapid progress has been made. Its degree of agreement with more traditional evidence from anatomical features is still being evaluated (Lafontaine and Fibiger 2006).

Morphological and molecular evidence agree that about 30% of the species of Noctuidae as here defined, including a majority of the major pests, belong to a clade (= monophyletic group) known as the "trifines." (The name refers to a feature of adult hindwing venation pointed out by Hampson.) There is also strong evidence that about half the trifines, in turn, belong to a clade, sometimes called the "true cutworms" (Lafontaine 1993), that subsumes nearly all of the subfamilies Xyleninae, Hadeninae, and Noctuinae of previous authors. These are provisionally placed with the Heliothinae and several smaller groups, also of significance as pests, in what has been termed the "Pest Clade" (Mitchell et al. 2006). Relationships among the remaining subfamilies, here informally termed the "lower trifines," are as yet poorly resolved.

Molecular data strongly support the inclusion of most of the remaining Noctuidae, some 23,000 species, in what has been termed the "L.A.Q." clade (Mitchell et al. 2006). As the acronym is meant to signify, this group consists of the traditional families Lymantriidae and Arctiidae plus most of the so-called "quadrifine" (as opposed to "trifine") Noctuidae in traditional classifications. Relationships are uncertain for two "quadrifine" groups not included in the "L.A.Q." clade, though the most recent results suggest that the Nolidae are related to the "trifines." Relationships within the vast "L.A.Q." clade, heretofore poorly understood, are now undergoing intensive molecular and morphological study (R. Zahiri, J. Zaspel, pers. comm.).

In addition to its importance for classification, a phylogeny is of cardinal utility in helping us understand how, and in what Earth-history context, the



Terminal Taxon	No. of spp.	Host growth form; main host taxa	Typical host range	Typical latitudinal distribution	# Neotrop/ # Nearctic spp.
Notodontidae	2800	Trees → (herbs) ; many families	oligo/poly	Trop (temp)	16.7
			oligo	Trop (temp)	
Euteliinae/ Stictopterinae	540	Trees; resin, latex plants	oligo	Trop (temp)	4.3
Hypeninae	500	Herbs (trees); many families	oligo/poly	Trop (temp)	16.7
Herminiinae	1000	dead leaves, fungi	(unknown)	Trop (temp)	16.7
Calpinae	2200	Trees,vines (herbs); Malvales, basal dicots	oligo(poly)	Trop (temp)	
Catocalinae	4500	Trees (herbs); many families	oligo(poly)	Trop (temp)	6.3
Hypenodinae	90	algae,lichens,fungi	(unknown)	Trop (temp)	
Eublemmini	375	Herbs (trees);Euasteridae	oligo(poly)	Trop (temp)	
Lymantriinae	2500	Trees (herbs); many families	poly(oligo)	Trop (temp)	5.6
Rivulinae	77+?	Herbs;grasses, sedges	oligo	Trop (temp)	
Arctiinae	11000	Herbs → (trees) → lichens	poly/oligo	Trop (temp)	20.0
Nolinae	1400	Trees (herbs); many families	olig (poly)	Trop (temp)	7.1
Plusiinae	400	Herbs; many families	poly(oligo)	Trop/temp	0.54
Raphiinae	12	Trees; Salicaceae	oligo	Temp	
Cuculliinae	250	Herbs [flowers, seeds]; Euasteridae	oligo	Temp	
Pantheinae	90	Trees; conifers; Rosidae	oligo	Trop (temp)	
Oncocnemidinae	100	Herbs [reprod. parts]; Euasteridae	oligo	Temp	
Agaristinae	600	Vines,Trees;Vitaceae, Onagraceae	oligo	Trop (temp)	2.8
Stiriinae s.s.	50	Herbs [reprod. parts];Asteraceae	oligo	Temp	
Amphipyrinae	35	Trees (herbs); many families	poly	Temp	
Feraliini	8	Trees; conifers	oligo	Temp	
Psaphidini	21	Trees; many families	poly/oligo	Temp	
Acronictinae	300	Trees → (herbs); many families	oligo(poly)	Temp (trop)	
Eustrotiini	630	Herbs; Poales, Euasteridae, others	oligo(poly)	Trop (temp)	
Acontiinae	1270	Herbs; Malvales, Asteraceae many others	oligo(poly)	Temp/Trop	
Elaphriini in part: *Galgula, Spodoptera*	42+?	Herbs; many families	poly(oligo)	Trop (temp)	
Condicinae	120	Herbs; Asteraceae	oligo	Trop (temp)	
Heliothinae	440	Herbs [reprod. parts];Euasteridae	oligo(poly)	Temp (trop)	0.07
Phosphilini	8	Vines; Liliaceae	oligo	Trop (temp)	
Eriopinae	120	Herbs; ferns	oligo	Trop (temp)	
Elaphriini in part: *Elaphria*	125+?	Herbs (trees); many families	poly(oligo)	Trop (temp)	
Anorthodes and relatives	350+??	Herbs (dead leaves); many families	poly	Temp/trop	
Noctuinae	1600	Herbs; many families	poly(oligo)	Temp (trop)	0.8
Glottulini	17	Herbs; Amaryllidaceae	oligo	Trop (temp)	
Other Hadeninae	2350	Herbs (trees); many families	poly(oligo)	Trop (temp)	1.8
Phlogophorini	170	Herbs; many families	poly	Temp/trop	
Xylenini in part	750	Trees; many families	poly(oligo)	Temp(trop)	0.4
Ufeini	6	Trees; Salicaceae	oligo	Temp	
Xylenini in part Apameini	570	Herbs; grasses & other monocots	oligo(poly)	Temp/trop	1.5

GUEST ESSAY ON OWLET CLASSIFICATION: CHARLES MITTER (UNIVERSITY OF MARYLAND) continued

enormous life history diversity of noctuids has evolved. Full exploration of this subject, barely begun, will require much new information on life history and phylogeny. A speculative example of the kind of insights that may emerge is provided by several broad differences in use of hostplants and geographic distribution between noctuid clades, visible in the phylogeny provided here (see detailed discussion in Mitchell et al. 2006). Although exceptions abound, the trifines appear to be predominantly herb feeders, whereas the remaining noctuids show a greater proportion of lineages feeding on trees, probably the ancestral habit for Noctuidae and most other so-called macrolepidopteran families. Trifines also show on average much greater association than other noctuids with open habitats, and with both high latitudes and high elevations (Holloway and Nielsen 1998). Accumulating evidence links these trends to the dramatic global climate changes of the Cenozoic era. Noctuids may have originated as tree feeders in the mesic to wet tropical forests that covered much of the earth starting early in the Cretaceous period (145–65 million years ago). Beginning about 50 million years ago, there has been an overall trend toward cooler and drier climates, latitudinal zonation of vegetation, and, particularly at higher latitudes, expansion of strongly seasonal and open habitats. The latter, in turn, prompted diversification of herbaceous angiosperm groups. While other moth lineages probably became increasingly restricted to the tropics, trifines and a few other insect groups (e.g., Winkler et al. 2009) seem to have been predisposed for adapting to this new ecological opportunity, analogous to the diversification of grazing mammals that accompanied the spread of open habitats including grasslands. These same habitats, of course, fostered the origins of human agriculture, pitting us against the trifines in a continuing global smackdown.

cocoons can sometimes be identified to genus and thus have value in a collection. There is a special need for data on the host ranges of introduced (nonnative) parasitoids employed as biological control agents (see text box page 31).

Owlet caterpillars are attacked by hundreds of invertebrate predators (Predators Plate): spiders, assassin bugs, predaceous stink bugs, lacewing larvae, ladybugs, ground beetles, sand wasps, vespid and related wasps, and ants. Yellow jackets, paper wasps, and ants are chronic threats to owlet larvae. Caterpillars that feed or take refuge on the ground are exposed to other enemies including centipedes and ground-dwelling spiders, ants, beetles, etc. The importance of mites that attack eggs and early instars is undoubtedly considerable but not well understood.

Caterpillars are a staple of songbirds and comprise the main, or in some cases, the sole food for both nestlings and adults (Holmes 1990; text box on page 9). As such, birds have been a major selective force in caterpillar evolution, influencing what caterpillars look like and how they behave. Birds have been implicated not only in what some caterpillars eat but also when and how they eat (Heinrich 1979, 1993). Rodents, especially mice, shrews, and voles, are caterpillar and pupa hunters, and replace birds in importance as predators of ground-dwelling caterpillars.

Classification and Nomenclature

The Noctuoidea is one of two hyperdiverse superfamilies of Lepidoptera, with world species diversity likely to exceed 75,000 species. It is rivaled only by the Pyraloidea whose tropical diversity, in places, seems almost unbounded. Given the extraordinary evolutionary success of the Noctuoidea, perhaps it is to be expected that the higher classification of the superfamily remains in a state of flux, even after more than a century of study and taxonomic shuffling. Commonly adopted classifications for the North American owlet fauna have drawn heavily from the framework established in Franclemont and Todd's (1983) checklist, which in turn was based on Hampson's (1898–1913) many works. A number of rearrangements to the Franclemont and Todd system were proposed by Poole (1995) in his phylogenetic treatment of the higher classification of the trifid noctuids. Recent studies on the classification of the superfamily have been fueled by studies of internal (especially male genitalia) and external morphology, immature stages, and molecular characters (e.g., Poole 1995; Speidel et al. 1996; Mitchell et al. 1997, 2000, 2006; Kitching and Rawlins 1998; Beck 1999, 2000; Fibiger and Lafontaine 2005; Lafontaine and Fibiger 2006; and Zahiri et al. 2011). Molecular data strongly suggest that two large lineages formerly regarded as full families, the tiger moths (Arctiinae) and tussock moths (Lymantriinae), derive from within the Erebidae. With but a handful of exceptions, we follow Lafontaine and Schmidt's (2010) North American checklist to arrange the species treated in this work. Their spellings for species names are also adopted. A summary classification appears below for those taxa represented here by one or more species. We selectively include tribes when these help to subdivide large subfamilies and/or heterogeneous subfamilies, e.g., Erebinae and Noctuinae. For a complete listing of the higher taxa within the North American Noctuoidea consult Lafontaine and Schmidt. Other authors treat subfamilies recognized in this work as full families: e.g., Mitchell et al. (2006) suggested that the Herminiinae, Hypeninae, and others could be given family-level status. The phylogenetic positions of many groups (e.g., Nolidae) may change, given the disagreement among existing studies. Due to the sheer enormity of the superfamily, and because many tropical, diminutive, and taxonomically isolated taxa have yet to be included in molecular studies, any treatmentmust be regarded as provisional—expect much taxonomic shuffling in the Noctuoidea over the coming decades.

Higher Classification for the Owlets Treated in this Work[4]

Family Erebidae Leach, [1815]
- Subfamily Lymantriinae Hampson, [1893] [omitted]
- Subfamily Arctiinae Leach, [1815] [omitted]
- Subfamily Herminiinae Leach, [1815]
- Subfamily Pangraptinae Grote, 1882
- Subfamily Hypeninae Herrich-Schäffer, [1851]
- Subfamily Rivulinae Grote, 1895
- Subfamily Scoliopteryginae Herrich-Schäffer, [1852]
- Subfamily Calpinae Boisduval, 1840
- Subfamily Hypocalinae Guenée, 1852
- Subfamily Scolecocampinae Grote, 1883
- Subfamily Hypenodinae Forbes, 1954
- Subfamily Boletobiinae Guenée, [1858]
- Subfamily Phytometrinae Hampson, 1913
- Subfamily Erebinae Leach, [1815]
  - Tribe Catocalini Boisduval, [1828]
  - Tribe Melipotini Grote, 1895
  - Tribe Euclidiini Guenée, 1852
  - Tribe Poaphilini Guenée, 1852
  - Tribe Ophiusini Guenée, 1837
  - Tribe Thermesiini Guenée, 1852
- Subfamily Eulepidotinae Grote, 1895

Family Euteliidae Grote, 1882

Family Nolidae Bruand, 1846
- Subfamily Nolinae Bruand, 1846
- Subfamily Chloephorinae Stainton, 1859
- Subfamily Risobinae Mell, 1943
- Subfamily Collomeninae Kitching & Rawlins, [1998]
- Subfamily Afridinae Kitching & Rawlins, [1998]

Family Noctuidae Latreille, 1809
- Subfamily Plusiinae Boisduval, [1828]
  - Tribe Abrostolini Eichlin & Cunningham, 1978
  - Tribe Argyrogrammatini Eich. & Cunning, 1978
  - Tribe Plusiini Boisduval, [1828]
- Subfamily Bagisarinae Crumb, 1956
- Subfamily Cydosiinae Kitching & Rawlins, [1998]
- Subfamily Eustrotiinae Grote, 1882
- Subfamily Acontiinae Guenée, 1841
- Subfamily Pantheinae Smith, 1898
- Subfamily Diphtherinae Fibiger & Lafontaine, 2005
- Subfamily Dilobinae Aurivillius, 1889
- Subfamily Balsinae Grote, 1896
- Subfamily Acronictinae Heinemann, 1859
- Subfamily Agaristinae Herrich-Schäffer, [1858]
- Subfamily Cuculliinae Herrich-Schäffer, [1850]
- Subfamily Oncocnemidinae Forbes & Franc., 1954
- Subfamily Amphipyrinae Guenée, 1837
  - Tribe Amphipyrini Guenée, 1837
  - Tribe Phosphilini Poole, 1995
  - Tribe Psaphidini Grote, 1896
- Subfamily Stiriinae Grote, 1882
- Subfamily Heliothinae Boisduval, [1828]
- Subfamily Condicinae Poole, 1995
- Subfamily Eriopinae Herrich-Schäffer, [1851]
- Subfamily Noctuinae Latreille, 1809
  - Tribe Pseudeustrotiini Beck, 1996
  - Tribe Elaphriini Beck, 1996
  - Tribe Prodeniini Forbes, 1954
  - Tribe Caradrinini Boisduval, 1840
  - Tribe Dypterygiini Forbes, 1954
  - Tribe Actinotiini Beck, 1996
  - Tribe Phlogophorini Hampson, 1918
  - Tribe Apameini Guenée, 1841
  - Tribe Arzamini Grote, 1883
  - Tribe Xylenini Guenée, 1837
  - Tribe Ufeini Crumb, 1956
  - Tribe Orthosiini Guenée, 1837
  - Tribe Tholerini Beck, 1996
  - Tribe Hadenini Guenée, 1837
  - Tribe Leucaniini Guenée, 1837
  - Tribe Eriopygini Fibiger & Lafontaine, 2005
  - Tribe Glottulini Guenée, 1852
  - Tribe Noctuini Latreille, 1809

[4] The backbone of the classification used in this work was reproduced from Lafontaine and Schmidt (2010). However, our concept of the Amphipyrinae differs. We treat the Stiriinae as a separate subfamily (not as a subordinate tribe within the Amphipyrinae), and we regard the Phosphilini to be part of the Amphipyrinae, not a tribe within the Noctuinae. Additionally, we believe the larval characters and biology of *Ufeus* are so divergent as to be worthy of tribal recognition. (Lafontaine and Schmidt (2010) treat the Ufeina as a subtribe within the Xylenini.) As noted previously, two recent additions to the Erebidae, the Lymantriinae (tussock moths) and Arctiinae (tiger moths), were treated in Wagner (2005).

About This Book

Each family, subfamily, and less frequently tribes and larger genera, are introduced with information about diversity and distribution and general interest tidbits, followed by an abbreviated diagnosis and life history notes. Tips for collecting and rearing are sometimes added at the end of an introductory section. Additional information is salted into the Remarks sections for the species within a given group. Members of a genus are usually listed in alphabetical order, except in large genera (e.g., *Catocala*, *Lithophane*, and *Zale*), where related species and/or those similar in appearance or habit are grouped.

Each species account begins with a common name followed by the scientific name. Many of the former are our own, and are often based on an English rendering of the scientific name or a derivation of a related British species. Recent synonyms (enclosed by parentheses and preceded by an equals sign) sometimes follow the scientific name. For those species where different common names have been applied to the caterpillar and adult, we often use the name for the larva and place the adult name in brackets after the scientific name. Additional common names are sometimes added to the brackets or mentioned in the Remarks section, although we make no effort to provide a full reporting of common names, which can be numerous for economically important species. Our use of common and scientific names is idiosyncratic. We generally supply both, but not always; for example, we often skip mention of the Latin name when it is an obvious derivative the common name (e.g., Bethune's Zale and *Zale bethunei*). We favor common names for familiar species but switch to Latin names when dealing with more difficult taxonomic matters, issues, or species. When mentioning a second species in an account other than the subject species, we apply boldface to draw attention to the fact that some included information applies to a second entity. We generally adopt the common name accepted by the Entomological Society of America and BugGuide, but propose replacement names where we regard the accepted names to be factually misleading or inappropriate based on current taxonomy, hostplant data, etc. Additionally, we propose new common names for a number of unfamiliar moths for which no common name has so far been applied. For several subfamilies, we abandoned nonsensical or poorly considered names and applied a uniform naming system to bring the common names in line with existing classifications, e.g., Hypeninae are dubbed snouts and Plusiinae are called loopers. Common names of moth species are capitalized.

Full species accounts include four sections: Recognition, Occurrence, Common Foodplants, and Remarks. In the **Recognition** section we provide a description of the last instar; especially useful characters are italicized. (For taxa with one or more close relatives in our fauna and when we are uncertain that our description is diagnostic, no features have been italicized.) Each description ends with a generous estimate of the caterpillar's length. If known, and where coloration differs from that of the final instar, we frequently note the appearance of the middle and/or penultimate instars. The Recognition section often includes mention of congeners or other species likely to be confused with the focal species.

The **Occurrence** section begins with a listing of habitats frequented by a given species followed by a synopsis of the range, usually beginning with the northwestern corner of the distribution and cycling clockwise. We have endeavored to summarize the North American range east of the hundredth meridian; occasionally, and especially for widespread species, we mention the western and southern range limits. By convention, the range is followed by a synopsis of the number of annual generations and phenology (seasonal activity). For most Lepidoptera, the number of generations and the overlap between generations increase as one moves southward where species begin activity earlier in the year and fly later into the fall. Unless noted otherwise, we emphasize the life cycle and phenology that would be expected from northern Georgia to southern Canada. This section concludes with an abbreviated assessment of a species' abundance.

Common Foodplants are listed for every species. We have not attempted to provide a complete listing of known host plants, especially for those species with catholic diets. Robinson et al. (2002, 2011) are the best single-source compendia for foodplant data. Other important sources include Forbes (1954, 1960), Crumb (1956), Prentice (1963), Tietz (1972), Ferguson (1975), Rings et al. (1992), Covell (2005), and Heppner (2007). Taxon-specialized references are listed in the boxes that introduce the subfamilies. For general feeders, hosts are listed in alphabetical order. When foodplant preferences are apparent, we make an effort to mention them. Common names for the plant hosts closely follow those provided by the USDA website PLANTS Database (http://plants.usda.gov/index.html), although we do adopt a few considered exceptions. For example, we continue to use the traditional sense of the genera *Aster* and *Solidago* because we do not find that the proliferation of newly proposed generic names helpful for understanding the owlet diets in this guide. When the common name of the foodplant is likely to be unfamiliar or ambiguous, we provide the host's scientific name parenthetically. Many of the host records are our own; only occasionally do we insert our initials (e.g., in instances where we deem our record to be significant).

The **Remarks** section is a potpourri of information on a species' life history, behavior, taxonomy, economic importance, and other observations likely to generate interest in or appreciation for the insect and its caterpillar. Notes on husbandry and tips on how to locate larvae are given here. Extensive unpublished data appear in this section. Information relevant to members of a given genus or group has sometimes been divided among the Remarks sections of related species. For example, if the overwintering stage is constant across a genus, mention of this may be made only once, either in the introductory box or in the Remarks section of the first member of the genus treated. Less obviously, when there was available space on a page, we frequently filled the Remarks section with information pertinent to other members of the focal species' genus, tribe, or even subfamily.

Making Identifications

Descriptions in this treatment apply to the last instar. Unfortunately, there is no easy way to know when an unfamiliar caterpillar is fully grown. We still occasionally fail to recognize last instars of very small species collected in the wild before

TRANSFORMERS

Caterpillar guides are given to treatments of the last instar, in large measure because this is the most conspicuous; in the case of pests, the last instar is the most destructive and therefore receives a lot of attention. For greater than half the species in this guide, our last-instar image will allow one to identify a penultimate or even a middle instar of that same species. But in others, remarkable changes in form and habit transpire between the nascent and mature larva. Those that we record for many daggers are especially noteworthy (pages 258–99)— differences between the last two instars may exceed those that occur between the genera and subfamilies of other moths. More remarkable still is that a few of these "masters of metamorphosis" even change their phenotype and *modus operandi* within a single instar. Take the case of the Greater Oak Dagger (*Acronicta lobeliae*) (below). The early and middle instars resemble leaf blemishes and rest near their feeding site. The pale last instar invariably rests off of foliage, on twigs, where its coloration is matched to oak bark. But late in the last instar the caterpillar changes yet again, transitioning to a black-headed, dark caterpillar with pale striping that resembles some *Datana* (Notodontidae). Our guess is that this is an adaptive form, suited to the ground and the business of tunneling into downed wood, the preferred pupation site. Even more remarkable changes occur in its distant kin, Cadbury's Mystique (*Comachara cadburyi*) (page 303) and the Hebrew (*Polygrammate hebraeicum*) (page 302).

they pupate. While one might generalize that many noctuoid caterpillars exceed 3 cm in length at maturity, the number of exceptions is legion; e.g., nolines are under 1.5 cm when mature, and hypenodines can be much smaller. For many species, we provide an ancillary image of the penultimate instar when its coloration differs significantly from that of the mature larva.

Familiarize yourself with the scope of this guide prior to using the work for identification purposes: flip through the species accounts, read the subfamilial and tribal boxes, and look over the images to develop a "gestalt or feel" for the major groupings. Conversely, when closing in on an identification, be sure to back up and read tribal and subfamilial boxes to make sure that your caterpillar possesses the features common to the group.

Variation in coloration and patterning is the rule, especially in the darts (Noctuini). Don't expect your caterpillar to exactly match any image; conversely, even when a caterpillar seems to be a match for a species figured here, make sure your unknown possesses the characters given in the diagnosis. Features such as head capsule shape, setal lengths and patterns, proleg development, and warting are less variable—these should mirror the features of your unknown. Keep in mind that some shape features, such as the form of the rump, are dependent on whether the caterpillar is ambulatory or at full rest. *Characters that we feel are especially reliable and helpful are italicized.*

In many subfamilies, knowledge of the foodplant will help reveal a caterpillar's identity. With unusual hosts, it is possible to zero in on an identification by working backward from the foodplant index. Do not assume that the plant on which you have found a caterpillar is the host; caterpillars wander. Make a point to check for recent feeding damage when you discover a caterpillar or, in the case where a caterpillar has been brought home, watch for signs of feeding and/or the production of feculae.

If you cannot find your caterpillar in this book, you might also consult works on the noctuoids of Europe and eastern Asia, e.g., Sugi (1987), Porter (1997), Beck (1999, 2000), and Ahola and Silvonen (2005, 2008, 2010). In many cases you will be able to get an approximate identification by checking these richly illustrated volumes.

Bug Guide (http://bugguide.net/node/view/15740), Moth Photographer's Group (http://mothphotographersgroup.msstate.edu/), and list serves can be powerful and immediate sources of help with troublesome larval (and adult) identifications. Cast around and do some homework before making posts—others are more likely to lend assistance when it is evident that a person has consulted easily accessible sources. Include pertinent data that can help in identification: host, date, and locality. Posts that contain such data and other observations serve a greater good.

Voucher Data and Specimens

For the majority of the species in this work, larval and adult specimen vouchers, original photographic images, rearing notes, and associated databases are those of the senior author and have been deposited at the University of Connecticut. Lesser numbers of larval and adult specimen vouchers are housed in the collections of DFS, Eric Quinter, and Tim McCabe. With the exception of 32 species loaned by Eric Quinter, all vouchers for the pinned adult images are at the University of Connecticut. The adult specimens imaged for this work bear the label "USDA Forest Service Noctuid Cater. Guide." Data for the adult images (state only) and figured larvae (locality, date, foodplant, collector, and photographer) are available from the senior author. While we endeavored to use images of larvae reared from eggs deposited by gravid females or wild-collected caterpillars that yielded identifiable adults, we have included images of caterpillars that were not successfully reared to the adult stage (for this reason and others, some images may be wrongly associated with a given species).

Diagnosing Owlet Caterpillars

Owlet caterpillars are fantastically rich in species and heterogeneous in form. No single character will ensure immediate recognition.[5] They range from slender to chunky, nearly glabrous to densely hairy, brown and nondescript to boldly aposematic, adorned in reds, yellows, or oranges. Setae may be straight or barbed. All have the crochets arranged in a series more or less parallel to the body axis (a **mesoseries**) (Fig. 9), never in a circle or incomplete circle. In most, the crochets are of a single length. Many have a midventral prothoracic gland, the **adenosma** (often visible as an everted tubular gland in preserved material). The head is usually smooth and rounded; a **coronal bar** to either side of the dorsal midline, and reticulate mottling over each lobe, are common. There are only two prespiracular (L group) setae on T1 (Fig. 10). In nearly all, there is only one SV seta on T2 and T3, although Arctiinae, some Plusiinae, and others have two (Beck 2009). Setae L1 and L2 on A3–A6 are usually below the level of the spiracle. The classic cutworm is smooth and stocky, with relatively short prolegs and reduced, inconspicuous setae; these are usually colored in earth tones. The SD1 seta on A9 is fine and hairlike (narrower in diameter than the width of the dorsal setae) in the cutworms and kin. Middorsal, subdorsal, and spiracular stripes are widespread. Conspicuously striped or ringed macrolepidopterans have a high probability of being owlets. Most have a full complement of prolegs (on A3, A4, A5, A6, and A10), although in some taxa the first, or first and second, pairs are either reduced or entirely absent.

It is easier to exclude taxa that are not owlets: none have branched spines (scoli) on the body or head. With the exception of the Green Marvel (*Agriopodes fallax*), they are not sluglike with minute secondary setae and the head is never fully retracted within the thorax (as in Lycaenidae and Limacodidae). If secondary setae are present, there is no anal point (between the anal prolegs, extending up toward the anus). Thyatirine drepanids, with two extra L group setae on A1–A8, come closest in appearance (see Wagner 2005: 141). The anal prolegs are not reduced, greatly lengthened, or otherwise modified, as is commonly the case with prominents (Notodontidae). The labral notch, which engages the leaf when a larva is feeding, is V-shaped in notodontids and usually U-shaped in erebids and noctuids.

In sum, if the crochets are arranged in a mesoseries, prolegs are present on A5, the anal prolegs are normal, and you have eliminated the common macrolepidopteran families as a possibility, you are probably looking at an owlet.

Keys to Owlet Larvae

Below we list works that include larval keys for large numbers of eastern North American species.[6] Full citations for each publication are given in the “Cited Literature” section at the end of this book. Works treating the larvae of subfamilies, tribes, or smaller numbers of species are mentioned in the introductory boxes for those taxa.

Crumb, S. E. 1956. Comprehensive treatment of North American owlet larvae with keys to most North American subfamilies, tribes, genera, as well as many species.

Forbes, W. T. M. 1954. Species keys for northeastern *Acronicta*, *Catocala*, *Zale*, and a few others; no familial or subfamilial key.

Godfrey, G. L. 1972. Keys and descriptions for approximately 45 genera and 150 species of North American Hadenini.

Godfrey, G. L. 1987. Key to about 70 species of commonly encountered North American owlets, including all major pest species.

Whelan, D. B. 1935. Key to 25 common pest species attacking corn in Nebraska; most are darts (Noctuini).

Supplemental Digital Resources

DLW’s website, linked at http://press.princeton.edu/titles/9420.html, includes an erratum and other ancillary resources to this book. Several owlets not treated in this work have accounts on the website. Others that appear here as abbreviated accounts have full accounts on the website. A draft key on the website will enable users to identify larvae of many eastern owlet caterpillars to subfamily and, in some cases, genus.

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[5] In Stehr’s (1987) key to the families of lepidopteran larvae, owlets appear in nearly a dozen places, all in the second half of his 225-couplet/triplet key.

[6] Beck’s (2000) key to European owlet caterpillars will work for many North American taxa, at least to the level of subfamily and tribe, and occasionally to genus.